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Patch-Scale Effects of an Invasive Ecosystem Engineer on the Structure and Function of a Eutrophic Stream

Samuel J. Hochhalter
Utah State University

PATCH-SCALE EFFECTS OF AN INVASIVE ECOSYSTEM ENGINEER ON THE STRUCTURE AND FUNCTION OF A EUTROPHIC STREAM

by

Samuel J. Hochhalter

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Approved:

_____	_____
Dr. Michelle A. Baker	Dr. Phaedra Budy
Major Professor	Committee Member
_____	_____
Dr. Edmund Brodie Jr.	Dr. Byron R. Burnham
Committee Member	Dean of Graduate Studies

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ABSTRACT

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by

Samuel J. Hochhalter, Master of Science

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Major Professor: Dr. Michelle A. Baker
Department: Biology

Recent theoretical and technological advances in ecosystem science have dramatically expanded the ways in which scientists can pursue and explore ecological questions. For my thesis research, I integrated the recent theoretical concept of organisms as ecosystem engineers with the relatively recent development of stable isotope tracer tests to ask the question: how does the invasive common carp affect stream ecosystem structure and function? To investigate the structuring role of carp, I measured autotroph seasonal distribution and abundance and macroinvertebrate seasonal abundance and diversity within two stream reaches in Spring Creek, Utah, USA; one with low carp biomass (LCB) and one with high carp biomass (HCB). I installed a series of carp exclosures in the HCB reach to examine the response of the stream to carp exclusion. To explore the effects of carp on stream nitrogen dynamics, I performed a three-week, continuous injection of ^{15}N as ammonium chloride.

The macrophyte and macroinvertebrate community was severely depauperate in the HCB reach compared to the LCB reach. The observed rapid colonization of a relatively abundant and diverse macrophyte and macroinvertebrate community at the carp exclusion sites in the HCB reach not only indicates that carp engineering reduces the abundance and diversity of these communities, but also highlights the importance of the spatial distribution of engineered and non-engineered patches in dictating the temporal scale of re-colonization. Carp engineering had a simplifying effect on stream N dynamics that ultimately limited the uptake and retention capacity of the HCB reach. For example, macrophytes played a dominant role in the N dynamics of the LCB reach by directly assimilating NH_4, retaining N rich FBOM, and by providing habitat necessary to support an abundant and relatively diverse macroinvertebrate community that facilitated greater trophic transfer of nitrogen. Conversely, carp reduction of macrophytes in the HCB reach resulted in an overall reduction in areal uptake rates of NH_4, reduced trophic transfer of N, and significantly reduced N retention. These results clearly indicate that carp engineering reduces macrophyte and macroinvertebrate abundance and diversity in streams and that N dynamics are simplified in carp engineered patches.

(101 pages)

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Samuel J. Hochhalter

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INTRODUCTION

Aquatic ecosystems have long provided humans with a source of drinking water, food, wastewater disposal, and recreation. As human populations continue to expand across the globe, demands and impacts on aquatic resources have escalated (Vitousek et al. 1997a). Ensuring that ecosystem services provided by freshwater can continue to be available for society while simultaneously protecting the natural integrity within these environments has become an increasingly important, albeit challenging aspect of natural resource management. Through the mandates of law (i.e., Clean Water Act), management agencies have been charged with the protection and restoration of the chemical and biological characteristics of freshwater ecosystems. Protecting and restoring natural integrity within streams is paramount not only to the long-term conservation of these systems but also in ensuring society will continue to benefit from freshwater resources.

Degradation of water quality in the form of nutrient enrichment is a prevalent issue facing society (Howarth et al. 1996). Additions of nitrogen (N) and phosphorous (P) into streams can have pronounced effects on ecosystem structure and function (Vitousek et al. 1997b). Nitrogen and P enrichment and subsequent eutrophication of streams not only alters the chemical integrity of these systems but acts to reshape nutrient demands (Earl et al. 2006), amplifies primary production (Smith et al. 1999) and ultimately restructure secondary and tertiary biotic assemblages (Jeppesen et al. 1998; Tammi et al. 1999; Wazniak et

al. 2007). Understanding the mechanisms driving nutrient cycling within freshwater systems is critical to informing the management and restoration of water quality and the biological communities in degraded stream ecosystems.

The physical template of streams (Valett et al. 1996; Alexander et al. 2000; Hall et al. 2003) and the microbial processes at the water-benthic interface (Hall and Tank 2003; Webster et al. 2003) have been considered the dominant factors driving biogeochemical cycles in streams. While these factors are clearly important, the activities of fish have emerged as a powerful mechanism by which nutrient cycles in lotic ecosystems are mediated (Flecker 1996; Vanni et al. 2002; Taylor 2005; Taylor et al. 2006; McIntyre et al. 2008). For example, the size structure and species assemblage of fish communities can create biogeochemical hotspots (McIntyre et al. 2008) and alter flow paths of nutrients (Schaus et al. 1997; Vanni et al. 2006) through trophic interactions and excretion of nutrients. Additionally, individual species can exert strong controls in biogeochemical cycles (Vanni et al. 2002) even in diverse, species-rich ecosystems (Flecker 1996; Taylor 2005; Taylor et al. 2006) by altering the abiotic aspects of streams.

The role of individual species has long been a focus in ecology. However, only recently has the concept of ecosystem engineers been unified as a major topic in ecology and ecosystem science (Jones et al. 1994, 1997). Ecosystem engineers by definition are organisms that modify the transfer, availability, and quality of materials and physical habitats within ecosystems (Jones et al. 1994, 1997). The number of studies addressing the role of ecosystem engineers since

the introduction of the concept has rapidly increased (Coleman and Williams 2002; Wright and Jones 2006), and numerous aquatic organisms have been identified as ecosystem engineers including aquatic vascular plants (i.e., macrophytes; Caraco et al. 2006), several invertebrate species (Stewart and Haynes 1994; Strayer et al. 1999; Gutierrez et al. 2003), and several fish species (Flecker 1996; Zambrano et al. 2001; Coleman and Williams 2002).

The effect of ecosystem engineers and especially those of invasive ecosystem engineers on aquatic resources is an area of much warranted concern. Invasive ecosystem engineers have been shown to alter biodiversity (Parkos et al. 2003), to shift biogeochemical cycles (Strayer et al. 1999; Hall et al. 2003), and to restructure habitat quality and quantity (Crooks 1998), often to the detriment of the ecosystems and the services they provide to human society (Zavaleta 2000).

The numerous mechanisms through which ecosystem engineers modify their surroundings and the myriad abiotic and biotic responses of the ecosystem to these modifications has prompted researchers to organize and outline approaches to investigate the role of ecosystem engineers in diverse habitats and ecosystems (Jones et al. 1997; Crooks 2002; Wright and Jones 2006). A framework for classifying the effects of invasive ecosystem engineers has been proposed by Crooks (2002) and is based on ideas originally put forth by Vitousek (1990). The framework states that exotic species may alter the “flow, availability, or quality of 1) nutrient resources within biogeochemical cycles, 2) trophic resources within food webs and 3) physical resources such as living space,

sediment, light, or water" (Crooks 2002). Additionally, Jones et al. (1997) recommend study designs that compare patches of ecosystems with and without the engineer in addition to manipulation of the engineered patch to mimic the absence of the engineer. Through integration of these frameworks, I investigated the effects of a prolific exotic fish, common carp (*Cyprinus carpio*) (hereafter called carp), on community composition and the flow, availability, and export of nutrients in a eutrophic stream in northern Utah, USA.

Native to Asia, the carp was originally introduced to North America in the mid 1800's as a commercial food fish (Fritz 1987). Rapid human transport of carp through both intentional (e.g., commercial food fish propagation) and unintentional (e.g., discarded bait) mechanisms has resulted in few temperate North American waters free of carp (Panek 1987). The astonishing invasive capabilities and subsequent extensive distribution of the carp is a product of their possession of many, if not all of the characteristics describing successful invaders (Panek 1987; Koehn 2004). High reproductive capacity, rapid growth, short generation time and broad environmental tolerances of carp frequently result in their prolific abundance and resilience within aquatic ecosystems (Panek 1987; Koehn 2004). These factors have led to carp being placed among the world's 100 worst invasive species (IUCN 2002).

Despite numerous studies on the impacts of carp invasions on lake ecosystems, little is known of their effects on stream ecosystems. Through ecosystem engineering, carp elicit considerable controls on lentic ecosystem structure and function (Parkos et al. 2003; Miller and Crowl 2006; Matsuzaki et

al. 2007) and may even alter lake steady state (Scheffer et al. 1993; Parkos et al. 2003). For example, carp bioturbation has been shown to reduce or eliminate macrophytes within experimental ponds (Roberts et al. 1995; Zambrano and Hinojosa 1999; Parkos et al. 2003) and natural lakes (Threinen and Helm 1954; Tryon 1954). In addition to physically dislodging macrophytes, increased turbidity due to carp resuspension of sediments reduces light penetration to the benthos (Roberts et al. 1995) which hinders macrophyte growth. Furthermore, carp excretion of nutrients promotes epiphyton growth which also further suppresses macrophyte growth (Williams et al. 2002; Matsuzaki et al. 2007). These feedback mechanisms can result in a transition away from a macrophyte dominated, clear water steady state to a turbid, phytoplankton dominated steady state (Scheffer et al. 1993; Parkos et al. 2003). Accordingly, the presence of carp, given our current understanding, is likely to confound management efforts aimed at maintaining and restoring water quality and the biological components of streams. As such, failure to recognize carp as a powerful ecosystem engineer capable of mediating nutrient dynamics and community structure within stream environments may thwart the best of water quality and ecosystem conservation efforts (Crooks 2002; Moore 2006; Parkos et al. 2003). A need therefore exists to determine the role of the invasive carp on stream ecosystem structure and function. As such, through my thesis research, I examined the effects of carp on:

1) Ecosystem Structure:

-epilithon and epiphyton ash-free drymass (AFDM) and chlorophyll *a* mass

-macrophyte distribution, drymass, AFDM, and species composition

-macroinvertebrate abundance and species composition

2) Ecosystem Function:

-nitrogen dynamics

-ecosystem metabolism

STUDY SITE AND STUDY DESIGN

Physical Setting

Spring Creek originates as a ground water upwelling in the middle of the Cache Valley northern Utah and has a drainage area of 75.9 km^2 (Figure 1). Spring Creek is classified as a class 3A cold water fishery by the state of Utah Division of Water Quality. Spring Creek suffers from nutrient loading from both point and nonpoint sources, which has proved critical in dictating the current chemical and biological characteristics of the stream (Utah DEQ 2002). Thus, the system is listed as impaired due to elevated levels of total phosphorous, ammonia, and temperature as well as having dissolved oxygen fluctuations in excess of state standards (Utah DEQ 2002). With the exception of water chemistry data, little data are available on Spring Creek especially regarding the physical and biological characteristics of the system.

Fish Community

The historical native fish assemblage of Spring Creek is largely unknown, however, the former distribution of Bonneville cutthroat trout (*Oncorhynchus clarki utah*), mountain whitefish (*Prosopium williamsoni*), large scale sucker (*Catostomus marcocheilus*) and mottled sculpin (*Cottus bairdii*) encompass the lower Little Bear River drainage suggesting these species likely inhabited Spring Creek in its pre-impaired state. Presently, several species of fish inhabit Spring Creek including brown trout (*Salmo trutta*) and sculpin (*Cottus sp.*), however, carp appear to dominate fish biomass in most reaches. The upper-most 680

meters of stream contains very few carp, as two summer and one winter visual assessment prior to initiation of this study failed to identify any carp within this reach. In further support of this observation, numerous carp are readily observable in all other stream reaches, and dense and widespread macrophyte stands are only present in the upper most reach. This fragmentation in carp distribution established the underlying study design of this research project.

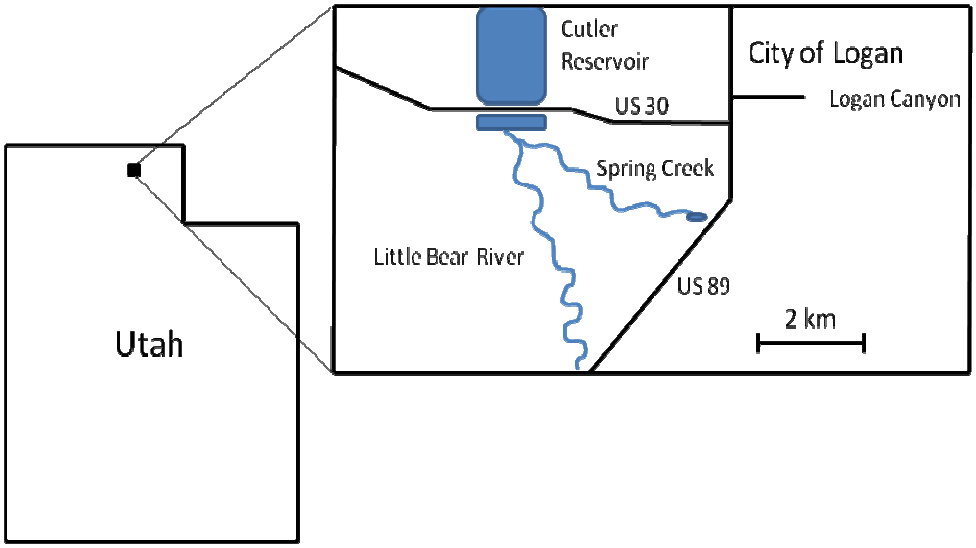

Figure 1: Map of central Cache Valley, Utah, USA depicting location of Spring Creek to relevant landmarks.

Study Design

Through my study, I addressed two levels of carp impacts on stream ecosystem structure and function per the recommendations of Jones et al. (1997). First, I compared biomass, nitrogen cycling and ecosystem metabolism in reaches located within 500 m of each other but that differed naturally in carp biomass - engineered versus non-engineered patches (Figure 2). These reaches

are hereafter defined as low carp biomass (LCB) and high carp biomass (HCB). Second, I installed 1X1 m carp exclosures in the HCB reach to elucidate effects of carp on benthic biomass and nitrogen retention within that reach – experimental manipulation to mimic the absence of the engineer.

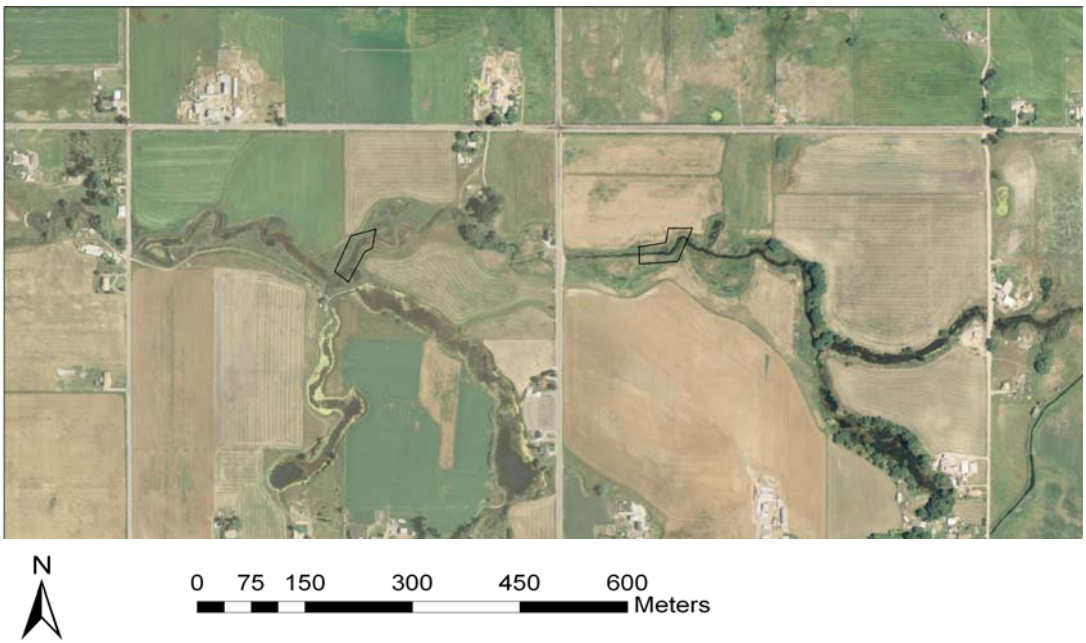

Figure 2: Aerial photograph of the section of Spring Creek, UT that contains the low carp biomass and high carp biomass study reaches. The right box outlines the low carp biomass reach and the left box outlines the high carp biomass reach. The creek flows to the west. Note the horseshoe shaped, man-made pond complex immediately to the south of the downstream reach. Photo credit: Andrew Hill, Utah State University.

The LCB reach originates from a spring pond and flows for 680 m. A representative 160 m study reach was designated approximately 400 m below the pond. Six sample stations located at meter marks -10, 10, 35, 65, 110, and

150 m were established with meter mark 0 representing the future site of a stable isotope injection. Spring Creek then flows through a culvert and has a narrow shaded channel reach. The HCB segment has its origin at the downstream end of this shaded segment. I established six sample locations (-10, 15, 35, 65, 115, 150 m) in a 160 m representative reach approximately 500 m below the termination of the LCB study reach. In general, riparian vegetation in each reach is limited to annual and perennial forbs, many of which are invasive (e.g., Common Teasel *Dypacus sylvestris*). As such, both stream reaches have open canopies with little to no riparian shading (Figure 3).

Figure 3: Pictures showing the 35 m sample location in the low carp biomass reach (on the left) and the 65 m sample location in the high carp biomass (on the right) of Spring Creek UT in mid-June, 2008. Note the difference in macrophyte distribution.

Planks and plank support structures were installed in late May, 2008 to allow for sampling sites without having to physically enter the stream and risk suspension of benthic sediments during the study (Figure 4). At each sampling location, a wooden support frame with four legs were installed in the stream channel with the top frame exposed approximately 5-15 cm above the water

surface. Once support structures were installed, a 3.6 m long and 30 cm wide plank was secured to the stream bank on one end with the opposite end placed on the support structure. Support structures and planks were made of 2x4 whitewood dimension lumber and planks were capped with 1 cm plywood.

To help alleviate confusion later, I have provided a temporal outline of the different sampling regimes used in the study. Spatial autotroph distributions within each reach were measured in mid-June and again in mid-October. Biomass samples to compare across the two reaches and the exclosure treatments were collected in mid-July, late July, and mid-October. Tissue samples for isotope composition analysis were collected on days 7, 14, 24, 56, and 84 of the study with day 1 being July 4th, the first day of the stable isotope injections, and day 24 being the day the injections were terminated. For reference, day 84 is in mid-October.

Exclosure Treatments

To mimic the absence of carp in a carp engineered patch, five 1.0 m^2 carp exclosures were installed at each sample location in the HCB reach. Exclosures were framed with four T-bar fence posts pounded into the substrate and were enclosed with metal garden fencing. Mesh size of the fencing was cut into 7x10 cm openings which was large enough to allow passage of native large scale suckers and small enough to prevent passage of common carp. Fencing was buried up to 20 cm into the stream substrate where feasible or secured with 15 cm long U-shaped pins if bed rock (the sediment deposits of the Pleistocene

Lake Bonneville) was reached prior to achieving a depth of 20 cm. To test for unforeseen exclosure effects, we installed partial exclosures adjacent to the full exclosure. Partial exclosures were simply a single panel framed by two T-bar fence posts connected with garden fencing as described above. The single panel was oriented perpendicular to stream flow and was situated at the upstream side of the 1.0 m^2 sample site. At each sample station in the HCB reach there was a full exclosure (hereafter referred to as inside exclosure treatment, IET), partial exclosure (PET), and outside exclosure (no fencing or posts, OET) sample sites (Figure 4). Exclosures were cleaned at least once daily during the injection and at least every other day after termination of the injection to remove debris buildup.

Figure 4: Picture of the exclosure treatments in the high carp biomass reach of Spring Creek UT, 2008. The picture is taken from the river left stream bank at the 150 m sample location. Direction of stream flow is from right to left.

METHODS

Measures of Ecosystem Structure

Physicochemical Parameters

Physical characteristics of each reach were described by measuring five geomorphic parameters: bankfull depth, wetted width, wetted depth, and water velocity. Fifteen transects were sampled systematically at 10 m intervals. Depth and velocity measurements were taken at three evenly spaced locations across each transect. Discharge at each reach was measured (four times prior to the start of the injection) with a Marsh-McBirney flow meter (Hach Company, Loveland CO). Stage rods were installed in each reach to allow for estimates of stream stage during the time frame spanning the tracer test. Stage-discharge relationships were established with direct discharge measurements and associated levels of the stage rod using regression analysis.

Paired water samples were collected systematically throughout the duration of the study; one unfiltered and one filtered. Filtered samples were filtered with pre-ashed Whatman (GF/F) glass fiber filters. All samples were collected in acid washed 125 or 60 ml HDPE Nalgene bottles and frozen until analysis. Unfiltered samples were analyzed for total phosphorous (TP) and total nitrogen (TN). Filtered samples were analyzed for phosphate (PO_4-P), nitrate (NO_3-N), ammonium (NH_4-N), and (Br^-).

All instruments used for analysis of water chemistry were calibrated using standard methodologies (APHA 1998). Quality control was implemented with

several methods including reagent blanks, spikes, check standards and duplicate samples. Total N was quantified using a potassium persulfate digestion (Nydahl 1978) followed by cadmium reduction for measurement of NO_3-N+nitite (NO_2-N; APHA 1998, EPA method 353.2). Measures of TP were made using a potassium persulfate digestion followed by an ascorbic acid molybdenum reaction for soluble reactive phosphorus (SRP, Murphy and Riley 1962, EPA method 365.1). Both colorimetric analyses were done on an automated analytical system with FASPac II data acquisition software (Astoria Pacific International, Portland OR). NO_3-N and Br^- concentrations in filtered samples were measured using ion chromatography (Dionex Sunnyvale CA). NH_4-N concentration was measured using an automated alkaline phenolhypochlorite reaction followed by spectrophotometric analysis (EPA method 350.1, APHA 1998, Solorzano 1969) on an automated analytical system with FASPac II data acquisition software (Astoria Pacific International, Portland OR). PO_4-P on filtered samples was measured using the ascorbic acid molybdenum reaction as outlined for digested TP samples above. All concentrations are expressed as mg/L.

Water was collected for ^{15}N analysis in 4 L containers at each sample location once prior to the start of the injection and on days 7, 14, and 23 and again 8 hours after termination of the injection. Samples were transported on ice to the lab where they filtered and prepared according to the methods of Mulholland et al. (2000).

Biological Compartments

Within Spring Creek, the major biological compartments consisted of fine benthic organic matter (FBOM), which, due to sampling logistics included episammon, the algae that grows on sediment; macrophytes; epiphyton, the algae that grows on macrophytes; macroinvertebrates; and fish. Floating mats of *Cladophora* were observed on stream margins and sampled when present.

Carp biomass - Estimates of carp abundance within each reach were obtained from multiple pass depletion estimates using a backpack electrofishing unit (Smith-Root, Ins. Vancouver Washington) within each stream reach in early June, late July, and mid-October. The LCB reach was sampled in its entirety (680 m) in June and October. To avoid disturbing the benthos and transporting ^{15}N labeled sediments downstream, we did not electrofish the LCB reach in July. The HCB reach was sampled in its entirety (480 m) in June and the lower 300m were sampled in July to avoid disturbance of the benthos within the section of the reach that contained our ^{15}N sample stations. Due to equipment malfunctions, the October electrofishing surveys of the HCB reach were limited to the lower 300 m.

Prior to sampling, I isolated the top and bottom of each reach with block nets or used hydrogeomorphic features (e.g., long shallow riffles) to preclude immigration into or emigration out of each reach during sampling. Fish were sampled with one to two backpack electrofishing units that conducted three consecutive passes starting at the downstream end of the reach. Upon capture, fish were placed in live cars until completion of the pass. To reduce handling

stress, fish were anesthetized with tricaine methanesulfonate (MS-222); anesthetized individuals were measured for total length and weight and then revived in a second live car. When all passes were complete, block nets were removed and fish redistributed throughout the reach. We did not capture sculpin and dace due to limitations of electrofishing in sampling small benthic species.

A maximum likelihood estimator was used to estimate abundance and associated variance estimates (Hayes et al. 2007). Abundance was extrapolated across the total wetted area sampled to acquire estimates of fish density. Fish density was expressed as g/m^2 and kg/ha to facilitate comparisons with values reported in the literature.

Spatial autotroph distribution - Percent cover of each autotroph compartment (filamentous algae, macrophytes, and cladophora) was measured at the reach-scale prior to the start of the injection in mid-June and again eight weeks after termination of the injection in mid-October. Two survey methods, a modified rapid assessment, and a view box method described in detail by Bowden et al. (2007) were employed. Each method was conducted at a total of 15 transects systematically spaced at 10 m intervals within each reach.

Surveys began at the farthest downstream end of each reach and proceeded upstream. The rapid assessment method involved three surveyors standing on the same side of the stream and each surveyor independently characterized the percent coverage of macrophytes, *Cladophora*, and filamentous algae (hereafter collectively referred to as benthic autotrophs) across the transect. After each surveyor had silently derived their values, each person

verbally stated them and the group then discussed and agreed upon a final composition value. We then stretched a tape measure across the transect and used a view box at three to five evenly spaced points across the transect to characterize benthic autotroph coverage. The same person performed all view box assessments to avoid differences in surveyor bias. The view box method was always performed after the rapid assessment method to avoid unintentional bias. Macrophyte voucher specimens were collected for all unique taxa observed and were preserved in a plant press and later identified to the genus or species level at the Intermountain Herbarium, Utah State University, Logan, Utah.

In addition to the reach-scale survey described above, the spatial distribution of benthic autotrophs at each exclosure treatment sites was recorded at the time of exclosure installation and again in late August with a view box.

Biomass of biological compartments - Total biological compartment biomass was derived from percent cover estimates described above, and measures of biomass per unit area described below. I measured biomass per unit area of FBOM, macrophytes, epiphyton and *Cladophora* in both reaches and within each exclosure treatment three times during the study as outlined in the time line above.

Fine benthic organic matter—Four metrics describing FBOM were measured: 1) ash free drymass (AFDM), a measure of the organic matter content of a sample; 2) the masses of carbon (C) and nitrogen (N); 3) the isotopic composition (^{13}C:^{12}C and ^{15}N:^{14}N ratios); and 4), the mass of chlorophyll *a* per

unit volume, often used as a surrogate measure of primary production (Steinman and Lamberti 1996). FBOM was sampled as part of the spatial coverage-biomass survey described above, weekly at each sample location during the ^{15}N experiment, and monthly thereafter as per the time line described above.

Fine benthic organic matter was sampled with a PVC pipe corer that had a diameter of 6 cm. The corer was placed to a maximum depth of 10 cm (Mulholland et al. 2000) at a randomly selected location and total depth of corer in the sediment and the depth of water inside the corer were measured. Sediments isolated by the corer were then vigorously stirred with a flat metal bar and all water and suspended sediment pumped into a collection bucket with a handheld manual bilge pump. Samples were homogenized inside the collection bucket and then subsampled into a single 120 ml aliquot. Samples were stored on ice for transport back to the lab. To avoid ^{15}N contamination across sites, we started at the lowest enriched sites and successively progressed to higher enriched sites. Additionally, collection buckets and bilge pumps were thoroughly rinsed with stream water between sample locations.

At the lab, three subsamples from each aliquot were filtered onto individually labeled, ashed, and pre-weighed 25 mm Gelman AE glass fiber filters. These were then placed in aluminum foil and frozen for later analysis.

For measures of AFDM, the first replicate sample was placed in an individually labeled, pre-weighed tin weigh boat. Samples were then dried at 60 C until a constant drymass was achieved (24-48 hours). The samples were then combusted in a muffle furnace at 450 C for 2 hours. After cooling, samples were

wetted with deionized water and re-dried at 60 C until a constant weight was achieved. Values derived from this process were then used to calculate the AFDM as the difference between dry mass and ashed mass.

To compare FBOM AFDM values across reaches, I used the mean values found for samples collected at the five OET sites in the HCB reach and those collected at the five sites in the LCB reach in mid-July, late July, and in mid-October. Similarly, these mean values were used to estimate reach-scale FBOM standing stock on days 24 and 84 of the study for use in the mass balance of injected ^{15}N.

For measures of C and N content as well as the ratio of ^{13}C:^{12}C and ^{15}N:^{14}N, the second replicate sample was dried at 60 C until a constant weight was achieved. Once dry, samples were encapsulated in tin capsules (Costech Analytical Technologies, Valencia CA), placed in a well plate and shipped to the Stable Isotope Facility at the University of California Davis (SIF, UC Davis). There, C and N content and isotopic composition were measured using a PDZ Europa ANCA-GSL elemental analyzer connected to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire UK).

Chlorophyll *a* was extracted from the third replicate sample using 90% ethanol. Extraction was conducted in the dark at 78 C for 5 minutes, followed by 24 h of refrigeration. Extracted pigments were analyzed by spectrophotometry at 665 and 750 nm wave lengths. Each sample was corrected for phaeopigments (deceased or inactive autotroph pigments) by adding 0.1 ml of 1 M HCl and re-

analyzing the sample at the above wave lengths (Steinman and Lamberti 2007). Data are expressed as mg Chl *a* per ml of sediment.

Macrophytes and floating cladophora mats - Measures of macrophyte and *Cladophora* biomass per unit area were obtained by harvesting a known area with a bottomless bucket. Samples were collected at three sites that had 100% coverage of the compartment and that were located downstream of the 150 m sample location within each reach. Upon collection, samples were placed in ziplock bags and transported on ice to the lab for further processing.

In the lab, each bottomless bucket sample of macrophytes was placed in a 5 L Nalgene bottle filled with 250 – 500 ml of tap water. Samples were vigorously shaken for 1 minute to dislodge macroinvertebrates and epiphyton (Cattaneo and Kalff 1980). After shaking, macrophytes were placed in a labeled ziplock bag and frozen for later measurements of dry mass. The epiphyton solution was sieved to remove invertebrates, measured for total volume, then filtered onto three individually labeled, ashed, pre-weighed 25 mm –Gelman AE glass fiber filters as described for FBOM. Samples and associated filters were placed in aluminum foil and frozen for later analysis of AFDM, C:N content, and for chlorophyll *a* concentration as described for FBOM.

During the ^{15}N experiment, the entire above ground portion of one individual macrophyte (*Potamogeton filiformis)* was collected weekly at each sample site and placed into a 1 L HDPE Nalgene bottle. The bottle was then filled with ~250 ml of stream water and stored on ice until arrival at the lab. In the

lab, macrophytes were shaken (as described above) to remove macroinvertebrates and epiphyton.

At the time of analysis, frozen macrophyte and *Cladophora* samples were thawed, placed in an aluminum foil pouch and dried at 60 C until a constant dry weight was achieved (24-48 hours). Once dry, macrophyte samples were ground with a mortar and pestle, homogenized, subsampled and encapsulated for isotope analysis at the SIF UC Davis as described above for FBOM. To avoid ^{15}N contamination, samples were prepared from lowest enrichment to highest (i.e., above injection site first, then from farthest downstream progressing upstream) and the mortar and pestle were cleaned with 90% ethanol between each sample.

At the end of the experiment (mid-October), all macrophytes at the exclosure treatment sites were destructively harvested, identified to species when possible, and weighed for drymass.

Epiphyton - Epiphyton processing was the same as that described for the FBOM samples except that values associated with these samples are expressed as g of epiphyton per g of drymass of macrophyte tissue from which the epiphyton was removed. Epiphyton samples were frozen until later analysis of AFDM, C:N content, and chlorophyll *a* were performed.

Macroinvertebrates—To test for differences in seasonal macroinvertebrate abundance between the two reaches, we collected three surber samples (base area of 30 cm^2 and collection mesh size of 250 um) during each of three sampling events; once prior to the start of the injection in mid-June, once at the

end of the injection in early August, and again two months after termination of the injection in mid-October. Surber samples were collected from representative sites downstream of the 150 m sample location within each reach. The three samples from each reach were pooled, placed in a whirl pack bag, preserved with 80% ethanol, and refrigerated for later identification to the lowest taxonomic level possible, enumeration, and measurement of dry mass.

To test for macroinvertebrate response to carp exclosure, two surber samples were collected from randomly selected locations within each of the exclosure treatment sites at the end of the experiment, prior to destructive harvest (mid-October) of macrophytes at each site. Samples from each treatment site were pooled, placed in whirl pack bags, preserved with 80% ethanol, and refrigerated for later identification and measurement of dry mass. To ensure sampling effort was held constant between the two reaches and to facilitate unbiased comparisons between reaches, we collected paired surber samples from five locations within the LCB reach. All macroinvertebrates were identified and sorted to the lowest taxonomic level possible and functional feeding groups assigned following (Merritt and Cummins (1996) and Thorp and Covich (2001). Samples were then dried at 60 C until a constant dry weight was achieved. Macroinvertebrate biomass was scaled up to be expressed as g of dry mass/m^2.

During the ^{15}N experiment, 8-12 individual macroinvertebrates of each functional feeding group (FFG) were collected during days 14, 24, and 84. Major FFGs used were collector/gatherers (CG), predators, and scrapers in the LCB

reach and CG for the HCB reach. Macroinvertebrates were collected from the FBOM samples in the HCB reach by sieving left over FBOM slurry from each sample site. Additionally, some macroinvertebrate taxa (e.g., Corixidae) were collected in the HCB reach with an aquarium net. Macroinvertebrates in the LCB reach were collected by picking a handful of macrophytes and rinsing macroinvertebrates into a sieve. Macroinvertebrates were transported alive in 60 ml centrifuge tubes filled with stream water to the lab where their guts were purged in aerated tap water for 24 hours. A 24 hour purge allows ample time for macroinvertebrate guts to be cleared of food and thus eliminates bias in the analysis of their ^{15}N signature (Dodds et al. 2000). Invertebrates were then placed in labeled scintillation vials and frozen for later analysis. Frozen invertebrates were dried at 60 C until a constant dry weight was achieved and were ground with a pestle and mortar. Ground tissue was subsampled, encapsulated, placed in a well-plate and shipped to SIF UC Davis for analysis of C and N content and isotope ratios.

Measures of Ecosystem Function

Nitrogen Dynamics

^{15}N tracer test - To measure nitrogen uptake, mineralization, and retention, we conducted a stable isotope tracer experiment in both reaches for 3 weeks in July 2008. We chose to inject ^{15}N in the form of ammonium chloride (NH_4Cl) because of increased biological demand for ammonium (Dortch 1990) allowing for less ^{15}N to be injected to achieve a detectable change in ^{15}N signature of

biological compartments relative to injecting a similar quantity of ^{15}N-nitrate and because Spring Creek is listed on the Utah Division of Water Quality's 303d list for elevated levels of ammonium. As such, outlining the pathways and fate of NH_4-N in Spring Creek will aid water quality managers in restoring water quality in Spring Creek.

Based on background NH_4-N concentrations and stream discharge we calculated the mass of ^{15}N to be injected into each stream reach each day to achieve an enrichment of the water column delta value of 500 ‰. A water enrichment target of 500 ‰, has been shown to be adequate in labeling most biological compartments (Mulholland et al. 2000; Simon et al. 2004).

The stable isotope injections were initiated on July 4th for both reaches and continued until July 27th for the LCB reach and until July 28th for the HCB reach. Pump rates throughout the duration of study did not deviate from the targeted rate of 10 ml/minute. Average injectate concentrations were 81.31 mg/L for the LCB reach and 90.35 mg/L for the HCB reach. A total of 27.125 grams of ^{15}N-NH_4Cl was injected into the LCB reach and a total of 31.226 grams were injected into the HCB reach.

Each day a total of 1.464 g of 99% ^{15}N-NH_4Cl and 310.83 g of bromide was mixed with 15 L of deionized water in a 20 L HDPE Nalgene carboys. Bromide was used as a conservative tracer to estimate groundwater dilution within each reach. A peristaltic fluid metering pump powered by 12 volt marine deep cycle batteries injected the solution into each stream reach at a rate of 10 ml/minute. The relatively large channel widths of Spring Creek precluded the

creation of a mixing pool in the stream channel (typical approach to mixing solutes with stream water) so I designed a multiple drip point injection system. Specifically, I spanned the wetted channel width with 7.5 mm diameter Tygon tubing that was punctured every 20 cm with pin sized holes. The distal end of the tubing was sealed with a ziptie and secured to a T-bar fencepost that was pounded into the stream substrate. The tubing was elevated ~30 cm above the water surface and had a total length of 4 m in the LCB reach and 2.5 m in the HCB reach. With this setup, solute was injected at even increments perpendicular to the direction of flow.

All water and benthic compartment samples were collected at six stations within each reach (see above for station locations, and sampling and analysis details).

Isotopic notation – I used three basic metrics of isotope signatures in collected samples will be used in calculating presented values. These are: 1) atom %, 2) R_{sample}, and 3) delta value. Atom % is calculated with the equation:

$$\text{Atom\%} = {}^{15}N / ({}^{15}N + {}^{14}N) * 100$$

where ^{15}N is the mass or concentration of ^{15}N in the sample and ^{14}N is the mass of ^{14}N in the sample. Both expressed as µg/g of sample for tissue samples and as µg/L of water for water samples.

R_{sample} is calculated with the equation:

$$R_{sample} = (\text{Atom\%}/100) / (1-(\text{Atom\%} / 100))$$

and is dimensionless.

The delta value is calculated as:

$$\text{Delta} = (R_{sample} / R_{standard} - 1) * 1000$$

where $R_{standard}$ is the proportion of atmospheric N that is ^{15}N (equal to 0.0036765). ^{15}N signatures of biological compartments will be expressed in delta values which have units of ‰.

Delta values of samples collected downstream of the injection site were corrected for background abundance by subtracting the delta ^{15}N value of the sample collected above the injection site from the value of each sample collected downstream of the injection site. All delta values presented will be adjusted in this manner so that they represent the change in delta value associated with the injected ^{15}N. Likewise, for estimates of compartment specific NH_4 uptake rates and for mass balance calculations I used atom % excess values:

$$\text{Atom \% excess} = \text{atom \%}_{sample} - \text{atom \%}_{background}$$

where atom %sample is the atom % of the enriched sample and $\%_{background}$ is the atom % of the background sample collected for that compartment.

Compartment-specific uptake – Macrophyte NH_4 uptake rates were calculated from modified equations in Mulholland et al. (2000). To calculate NH_4 uptake rates, several additional calculations were necessary:

$$\text{Atom ratio of water} = 1 / ((1 / R_{sample}) + 1)$$

where R_{sample} is that calculated for water on day 7 of the injection.

The total mass of ^{15}N in the compartment is calculated by:

$$\text{Total } ^{15}N \text{ in compartment} = (DM_{100} * C * A * PN * PN\text{-}15N)$$

where DM_{100} is the drymass of the compartment at 100 % coverage, C is the proportional coverage of the compartment at the station, A is the total area of the

station, PN is the proportion of drymass that is N, and PN-^{15}N is the proportion of N that is injected ^{15}N.

Compartment-specific uptake rate for the entire station can then be calculated by:

NH_4 uptake for station (mg/day) = T-^{15}N / (AR * d)

where T-^{15}N is the total ^{15}N in the compartment at that station, AR is the atom ratio of water at that station and day, and d is the day of the injection.

Finally, compartment-specific areal uptake rates can be calculated by:

NH_4 uptake $rate_{compartment}$ (mg/m^2/day) = $U_{station}$ / A

where $U_{station}$ is the compartment-specific uptake rate of the station and A is the area of the station.

Uptake rates calculated from this approach tend to under estimate “true” uptake rates as N is often lost from biomass via turnover (Mulholland et al. 2000). Thus, to more accurately measure uptake rates, a turnover correction factor is needed. Compartment-specific uptake rates presented in this paper were corrected for turnover following the equations of Mulholland et al. (2000). The turnover rate (k) is calculated as the negative slope of the regression line for the plot of the natural log of the delta ^{15}N values of a compartment at the upper most site (10 m for LCB and 15 m for HCB) over time. This equation assumes a first order decay rate in the delta ^{15}N signature. From this, the turnover correction factor is calculated:

Turnover correction factor = (d * k) / (1 – $e^{-d * k}$)

where d is day of the injection and k is the tracer ^{15}N turnover rate.

Turnover time in days is calculated by:

$$\text{Turnover time (days)} = 1 / k$$

NH_4-N uptake rates corrected for turnover are calculated by:

$$NH_4 \text{ Uptake rate } (mg/m^2/day) = U * T$$

where U is the uncorrected NH_4 uptake rate for the target compartment and T is the turnover correction factor for the compartment.

Nitrogen mass balance – Mass balance of ^{15}N added was calculated by multiplying the background-corrected proportion of ^{15}N in a specific compartment (atom percent excess) by total compartment biomass. Mass balance was calculated for days 24 and 84 with day 24 representing total compartment uptake at the end of the injection and day 84 representing what I will call long-term (8 weeks) retention of added ^{15}N.

Ecosystem Metabolism

Rates of ecosystem metabolism were calculated from daily oxygen (O_2) budgets for each reach. In general, the change in dissolved oxygen concentration over a measurement interval is due to gross primary production, community respiration, and reaeration:

$$\Delta DO = GPP - CR \pm \text{reaeration}$$

where ΔDO is the change in dissolved oxygen concentration over a 24 hour period, GPP is gross primary production, and CR is community respiration, and reaeration is O_2 exchange between the water column and atmosphere (Young et al. 2008).

Gross primary production is the process by which autotrophic organisms convert solar energy into chemical energy. Primary production consumes inorganic molecules (e.g., carbon dioxide, CO_2) and converts them to organic molecules (e.g., plant and algal tissue), releasing O_2 as a byproduct. Community respiration is essentially the reverse of GPP in that heterotrophic organisms oxidize organic matter which consumes O_2 and releases CO_2.

DO and temperature were recorded at 30 minute intervals with a Troll 9500 sonde (In Situ Inc., Fort Collins Colorado) placed in the middle of each reach. Sondes were deployed for nine days in late July.

Reaeration was modeled using the relationship between the rate of DO change relative to the DO deficit during the night (Young et al. 2008). DO deficit is stream O_2 saturation relative to the atmosphere where negative values indicate the stream is losing O_2 to the atmosphere and positive values indicate the stream is receiving O_2 from the atmosphere.

Ecosystem metabolism in streams is often summarized with the production to respiration ratio (P:R) where values greater than one indicate that more organic material is produced by autotrophic organisms over a 24 hour period than is consumed by heterotrophic organisms. In this situation the stream is said to be autotrophic. Alternatively, P:R values less than one suggest less organic material is produced than is consumed over a 24 hour period and thus the stream is heterotrophic. Heterotrophic streams often rely on external or allochthonous energy inputs.

Rates of ecosystem metabolism were summarized for each reach by calculating the P:R ratio, GPP, CR, and net ecosystem metabolism (NEM; NEM=GPP-CR) for each of the nine days the sondes were in the stream.

Statistical Analyses

Students T-tests were used to test for differences in physicochemical parameters and ecosystem metabolism parameters between the two reaches. Students T-tests were also used to test for differences between the two spatial autotroph distribution survey methods. Alpha levels were set at 0.05.

To compare differences in compartment biomass and spatial distribution across reaches and time, I used repeated measures analysis of variance (ANOVA). For spatial distribution of autotrophs I considered differences significant at the 0.05 alpha level. Given low sample sizes (n = 3 and 5), I considered differences in compartment biomass per unit area significant at the 0.1 alpha level.

To compare differences in variables measured across exclosure treatments and time, I used repeated measures ANOVAs. Macrophyte biomass and distribution and macroinvertebrate numbers and biomass response to exclosure treatments were analyzed with three-way, fully crossed factorial ANOVAs. Differences in macrophyte and *Cladophora* NH_4 uptake rates across weeks, reaches, and exclosure treatment sites were analyzed with repeated measures ANOVAs. Alpha levels were set at 0.1 because of low sample sizes.

Normal quantile plots, histograms, and box plots were used to visually test for the assumption of normal distribution. Plots of residuals versus predicted values and residuals versus observed values were used to visually test for the assumption of homoscedasticity. In the event a violation of assumptions was identified, data were transformed. I corrected for post hoc multiple comparisons with the Tukey method for repeated measures ANOVAs and used the REGWQ method for factorial ANOVAs.

RESULTS

Measures of Ecosystem Structure

Physicochemical Parameters

All physical parameters were significantly different between the two reaches (Table 1). Specifically, the LCB reach was approximately 50% narrower, 25% deeper with slower average velocity. Dissolved nutrient concentrations were significantly higher in the LCB reach with the exception of PO_4 which was similar among the two reaches. Stage height within each reach varied little over the study duration with the exception of the LCB stage increasing in height in response to increases in macrophyte abundance in early July. Discharge in early July, however, did not increase (320 L/second in late-June to 321 L/second in mid-July).

Biological Compartments

Carp biomass - Carp biomass estimates varied by reach and season (Table 2). Unfortunately, an estimate of carp biomass in the LCB reach for June was not possible because four of the six carp were captured on the second pass; capturing more fish on a successive pass renders a depletion estimate invalid (Hayes et al. 2007). Therefore the biomass estimate for the LCB reach in June does not have an estimate of variance and should be interpreted with caution. In general, the biomass estimates of carp in the HCB reach across all seasons were substantially higher than those for the LCB reach. Carp biomass in HCB reach peaked in July, where they were 74% higher than estimates found in June

and 66% higher than the October estimate. The October electrofishing survey in the LCB reach captured a total of one carp, and thus no variance estimate was possible.

Table 1: Physicochemical parameters of the low carp biomass and high carp biomass study reaches in Spring Creek, 2008. P-values are from t-tests performed for each paramenter.

	LCB	HCB		
Physicochemical Parameter	Mean ± SE	Mean ± SE	p-value	Transformation
Wetted Width (m)	6.6 ± 0.47	12.37 ± 0.4	0.0001	none
Wetted Depth (m)	0.41 ± 0.02	0.3 ± 0.03	0.008	log
Velocity (L/second)	0.13 ± 0.01	0.2 ± 0.02	0.005	log
NH_4-N (mg/L)	0.015 ± 0.0005	0.012 ± 0.001	0.05	none
NO_3-N (mg/L)	0.95 ± 0.013	0.88 ± 0.016	0.003	none
PO_4-P (mg/L)	0.003 ± 0.0006	0.002 ± 0.0001	0.28	log
TN (mg/L)	1.16 ± 0.031	1.06 ± 0.007	0.02	log
TP (mg/L)	0.014 ± 0.001	0.0096 ± 0.0002	0.004	log

Table 2: Biomass estimates for common carp *Cyprinus carpio* in the low carp biomass and high carp biomass study reaches of Spring Creek, 2008. Data are mean ± standard SE.

	LCB			HCB		
Month	Population Estimate	g/m2	kg/ha	Population Estimate	g/m2	kg/ha
June	6	4.6	45.96	23.43 ± 0.81	13.29 ± 0.69	132.92 ± 6.88
July	-	-	-	72.08 ± 0.14	51.03 ± 0.14	510.3 ± 1.16
October	1	0.68	6.76	32.22 ± 0.8	22.34 ± 0.68	223.4 ± 6.83

Spatial autotroph distribution - Differences in the spatial distribution of autotrophs were striking between the two reaches. Most notably, macrophyte spatial coverage comprised an average of 62.2 % of the benthos within the LCB reach in mid-June and 78.2 % in mid-October, while macrophytes were relatively sparse in the HCB reach at only 10.9 % and 6.2 % between June and October, respectively (Table 3).

Table 3: Spatial distribution of autotrophs in the low carp biomass and high carp biomass reaches of Spring Creek, UT during mid-June and mid-October 2008. FA is filamentous algae, BS is bare sediment, VB is the view box method, and RA is the modified rapid assessment method.

Date	Reach	Method	% Macrophyte	% Cladophora	% FA	% BS
June	LCB	VB	62.18 ± 4.56	7.2 ± 2.09	6.43 ± 2.17	21.14 ± 3.45
June	LCB	RA	68.27 ± 7.25	4.53 ± 2.25	4.73 ± 2.72	22.87 ± 4.54
June	HCB	VB	11.05 ± 1.96	0	12.21± 2.66	76.96 ± 2.81
June	HCB	RA	12.23 ± 3.82	0	9.08 ± 3.08	78.69 ± 4.22
October	LCB	VB	77.8 ± 5.06	0	2 ± 1.29	20.09 ± 4.57
October	LCB	RA	83.8 ± 3.13	3.53 ± 1.44	0.33 ± 0.33	12.47 ± 2.72
October	HCB	VB	5.98 ± 1.55	0.56 ± 0.56	2.16 ± 1.23	91.31 ± 2.06
October	HCB	RA	3.46 ± 0.62	0.32 ± 0.12	5.64 ± 3.52	90.57 ± 3.47

As a result, exposed FBOM comprised the bulk of the benthos within the HCB reach throughout the study duration. The two methods used to survey the distribution of autotrophs yielded similar results (Table 4). For example, t-tests indicated that the two methods did not differ within a given reach and month, and both methods yielded similar results on within reach change in macrophyte coverage across July and October.

Table 4: Comparison of two autotroph spatial coverage survey methods and their ability to detect a change in macrophyte distribution in study reaches within Spring Creek, UT, 2008. VB is the view box method and RA is the modified rapid assessment method. P-values are from t-tests.

Reach	Month	Difference between methods	VB difference in macrophyte cover across months	RA difference in macrophyte cover across months
		p-value	p-value	p-value
LCB	June	0.57	0.03	0.06
LCB	October	0.56	-	-
HCB	June	0.41	0.17	0.18
HCB	October	0.57	-	-

The spatial distribution of macrophytes, filamentous algae, and bare sediment at the three exclosure treatment sites in the HCB reach did not differ at the time of exclosure installation (p = 0.67, 0.95, and 0.23, respectively; Figure 5).

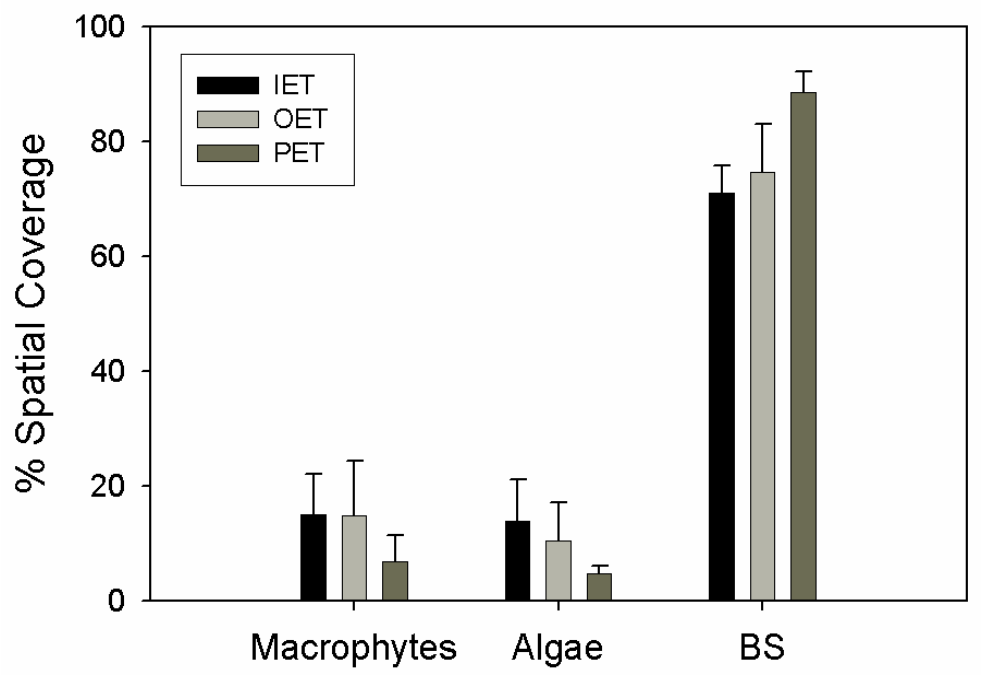

Figure 5: Spatial distribution of autotrophs at exclosure treatment sites in the high carp biomass reach of Spring Creek, UT at the time of exclosure installation in late May, 2008. Data are mean ± standard error SE. BS is bare sediment.

I observed a significant increase in the spatial distribution of macrophytes was observed at the IET sites from the time of exclosure installation in late May to late August relative to the outside and partial macrophyte distributions (p-value = 0.009; Figure 6). There was no difference in macrophyte spatial distribution between the OET and PET sites (p >0.1). Filamentous algae distribution did not change during this time period at any of the three treatments while bare sediment distribution declined as macrophyte distribution increased within the IET sites.

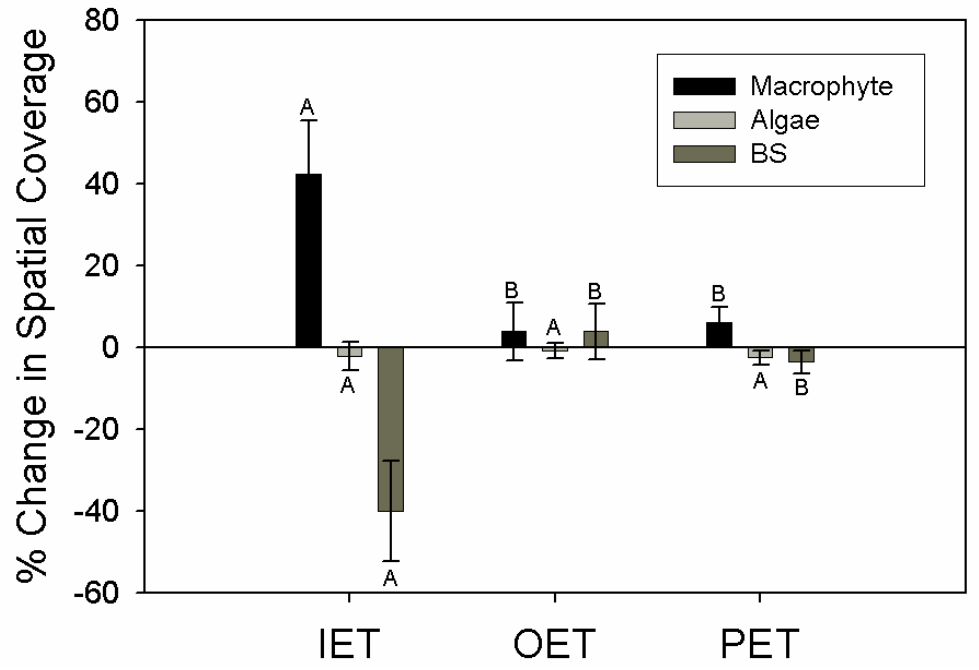

Figure 6: Percent change in autotroph distribution at the inside (IET), outside (OET), and partial (PET) exclosure treatment sites from the time of exclosure installation in late May to late August, 2008 in the high carp biomass of Spring Creek, UT. Bars with different letters within each autotroph category indicate a significant change at the 0.05 alpha level.

Fine benthic organic matter - AFDM and chlorophyll *a* concentrations were highly variable in both the LCB and HCB reaches as evidenced by the large standard errors associated with estimated means (Tables 5 and 6). With that said, FBOM AFDM per unit area did not differ significantly between the two reaches during the first sample event in late July (Table 5). Unfortunately, the mid-October LCB FBOM filters were lost, and thus mid-October comparisons were not possible. FBOM AFDM per unit stream area decreased from July to

October in the HCB reach, but this reduction was not statistically significant (p-value = 0.13).

FBOM chlorophyll *a* concentrations per unit stream area were highly variable and no significant differences between the two reaches were observed during either of the two sample events (Tables 5 and 6). In general, FBOM chlorophyll *a* concentrations decreased from late July to mid-October.

FBOM AFDM responses to exclosure treatments were variable within all three exclosure treatment types and over time (Tables 6, 7, and 8).

Table 5: Biomass of five biological compartments during late July 2008 in the low carp biomass and high carp biomass study reaches of Spring Creek, UT.

Late July	LCB	HCB	
Biological Compartment (g/m^2)	Mean ± SE	Mean ± SE	p-value
FBOM (AFDM)	196.63 ± 29.04	204.88 ± 39.75	0.99
FBOM (chlorophyll a)	0.35 ± 0.15	0.71 ± 0.23	0.97
Epiphyton (AFDM)	3.89 ± 1.5	0.29 ± 0.05	0.07
Epiphyton (chlorophyll a)	0.013 ± 0.0005	0.001	-
Cladophora (DM)	11.68 ± 0.34	32.45 ± 3.34	0.004
Macrophytes (DM)	74.42 ± 9.58	4.56 ± 0.55	0.002
Macroinvertebrates (DM)	6.78 ± 2.89	0.05 ± 0.03	0.0001

Table 6: Biomass (as ash-free drymass (AFDM); chlorophyll *a*; and/or dry mass (DM)) of five biological compartments during mid-October 2008 in the low carp biomass and high carp biomass study reaches of Spring Creek, UT.

Mid-October	LCB	HCB	
Biological Compartment (g/m^2)	Mean ± SE	Mean ± SE	p-value
FBOM (AFDM)	-	48.35 ± 7.42	-
FBOM (chlorophyll a)	0.53 ± 0.15	0.39 ± 0.19	0.7
Epiphyton (AFDM)	6.69 ± 3.51	-	-
Epiphyton (chlorophyll a)	0.019 ± 0.008	-	-
Cladophora (DM)	-	-	-
Macrophytes (DM)	86.37 ± 8.57	5.92 ± 0.24	0.0001
Macroinvertebrates (DM)	10.77 ± 0.85	0.013 ± 0.008	0.0001

In general, no significant differences were found in FBOM AFDM between the three treatment types within a given sample event with the only exception being the mid-October OET value was significantly less than the PET value (p-value = 0.03; Figure 7). Within the PET sites, FBOM AFDM increased in abundance from mid-July to late July (p-value = 0.01). FBOM AFDM abundance decreased significantly from late July to mid-October at the OET sites (p-value = 0.001). All other comparisons within a given treatment type across time were not statistically significantly different.

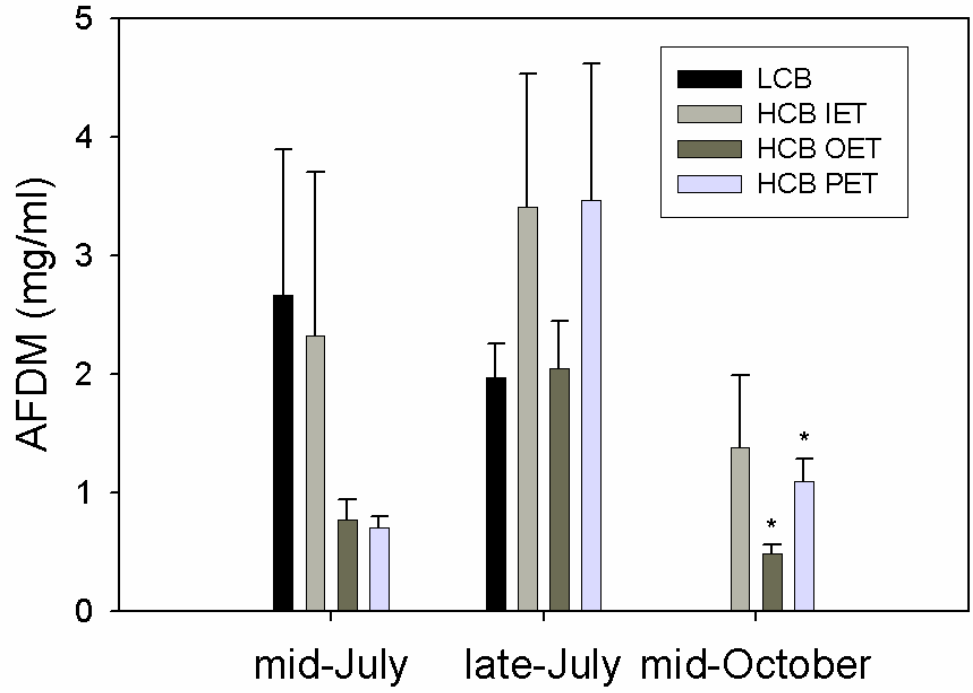

Figure 7: Fine benthic organic matter ash free dry mass in the low carp biomass reach and at the inside (IET), outside (OET), and partial (PET) exclosure treatment sites in the high carp biomass reach of Spring Creek, UT. Bars with asterisks above them are significantly different at the 0.1 alpha level.

Table 7: Mid-July, 2008 biomass and autotroph pigments (mean ± standard error, SE) of five biological compartments in the three exclosure treatments of the high carp biomass reach in Spring Creek, UT.

mid-July	Exclosure Treatment						
	Inside	Outside	Partial	I-O	I-P	O-P	
Biological Compartment	Mean ± SE	Mean ± SE	Mean ± SE		p-value		Transformation
FBOM (mg/ml)	2.33 ± 1.38	0.91 ± 0.28	0.7 ± 0.1	0.97	0.94	1	log
FBOM (mg chlorophyll *a*/ml)	0.002 ± 0.0006	0.0015 ± 0.0009	0.0008 ± 0.0002	0.97	0.92	1	log
Epiphyton (mg AFDM/g DM of macrophyte)	110.24 ± 40.67	54.76 ± 42.96	62.76 ± 20.2	0.77	0.99	0.96	log
Epiphyton (mg chlorophyll *a*/g DM macrophyte)	0.35 ± 0.09	0.25 ± 0.03	0.34 ± 0.16	0.99	1	0.99	none

Table 8: Late July, 2008 biomass and autotroph pigments of five biological compartments in the three exclosure treatments of the high carp biomass reach of Spring Creek, UT.

late July	Exclosure Treatment						
	Inside	Outside	Partial	I-O	I-P	O-P	
Biological Compartment	Mean ± SE	Mean ± SE	Mean ± SE		p-value		Transformation
FBOM (mg/ml)	3.41 ± 1.13	2.05 ± 0.4	3.466 ± 1.1548	0.92	1	0.9	log
FBOM (mg chlorophyll *a*/ml)	0.0067 ± 0.002	0.007 ± 0.002	0.00305 ± 0.0009	1	0.63	0.67	log
Epiphyton (mg AFDM/g DM of macrophyte)	90.04 ± 3.25	86.41 ± 32.4	77.2016 ± 37.5532	0.99	0.99	1	log
Epiphyton (mg chlorophyll *a*/g DM macrophyte)	0.44 ± 0.05	0.38 ± 0.08	0.39 ± 0.17	1	1	1	none
Macrophytes (%cover)	42.35 ± 13.22	3.15 ± 7.07	6.1 ± 3.78	0.009	0.009	>0.1	none

Table 9: Mid-October, 2008 biomass and autotroph pigments of five biological compartments in the three exclosure treatments of the high carp biomass reach of Spring Creek, UT.

mid-October	Exclosure Treatment						
	Inside	Outside	Partial	I-O	I-P	O-P	
Biological Compartment	Mean ± SE	Mean ± SE	Mean ± SE		p-value		Transformation
FBOM (mg/ml)	1.38 ± 0.61	0.48 ± 0.07	1.1 ± 0.19	0.91	1	0.03	log
FBOM (mg chlorophyll *a*/ml)	0.0038 ± 0.001	0.004 ± 0.002	0.0015 ± 0.0004	0.99	0.99	1	log
Epiphyton (mg AFDM/g DM of macrophyte)	65.42 ± 30.87	137.57 ± 32.65	116.71 ± 43.58	0.99	1	0.99	log
Epiphyton (mg chlorophyll *a*/g DM macrophyte)	0.88 ± 0.14	0.74 ± 0.23	0.83 ± 0.11	0.99	1	1	none
Macrophytes (g/m2)	60.12 ± 11.88	4.44 ± 1.49	7.49 ± 4.59	0.004	0.004	>0.1	log
Macroinvertebrates (g/m2)	0.42 ± 0.21	0.017 ± 0.01	0.021 ± 0.008	0.005	0.005	>0.1	log10

Like AFDM, FBOM chlorophyll *a* concentrations were highly variable across treatment types and time (Tables 7, 8, and 9). Unlike FBOM AFDM, no significant differences were found across the three treatment types during any of the sample events (Figure 8). The only significant difference found was an increase in chlorophyll *a* concentration from mid-July to late July within the IET and OET sites (p-values = 0.08 and 0.01, respectively). In general, FBOM chlorophyll *a* concentrations were lowest in mid-July, highest in late July, and intermediate in mid-October for all three treatment types.

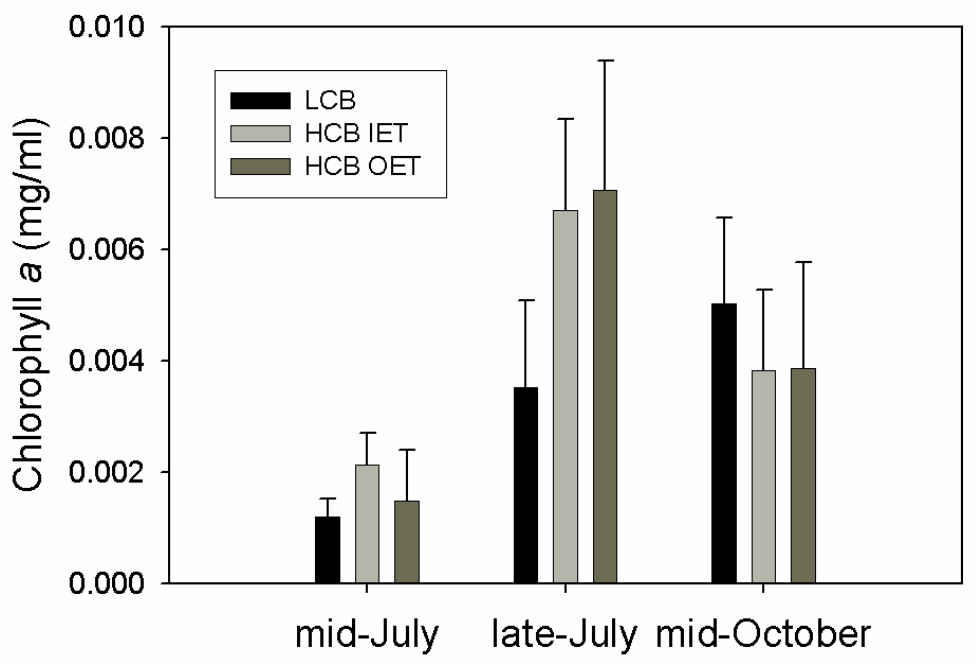

Figure 8: Fine benthic organic matter chlorophyll *a* mass per ml of FBOM in the low carp biomass reach and at the inside, (IET) and outside (OET) exclosure treatment sites in the high carp biomass reach of Spring Creek, UT. Partial exclosure treatment sites did not differ from the IET or OET sites so were excluded from the graph.

Macrophytes and floating Cladophora mats - Macrophyte dry mass per unit area was 16.3 times greater in the LCB reach during July and 14.6 times greater in mid-October than in the HCB reach (p-value = 0.0001; Tables 5 and 6). This difference is further accentuated when biomass of macrophytes per unit area was extrapolated to the reach scale –144.2 times greater in the LCB reach than in the HCB reach in late July and 56.1 times greater in mid-October. Macrophyte AFDM per unit area was 5.4 times greater in the LCB reach than in the HCB reach in July and 12.2 times greater in October. In contrast to macrophyte distribution, floating *Cladophora* mat dry mass per unit area was 2.78 times greater in the HCB reach than in the LCB reach in July (Table 4, p-value = 0.0008). Because the distribution of *Cladophora* mats was substantially greater in the LCB reach than in the HCB, in July the reach scale total drymass of *Cladophora* mats was 31.5 times greater in the LCB reach. Floating *Cladophora* mat distribution in October was minimal in both reaches, and thus samples were not collected.

In concordance with the spatial distribution response, macrophyte biomass response at the IET sites was significantly greater than both the OET and PET sites (p-value = 0.005; Figure 9). The OET and PET site macrophyte biomass responses were not significantly different (p-value >0.1).

In addition to a significant biomass response, five of the seven macrophyte species found within the LCB reach colonized the IET sites, whereas only two of the seven species were found at the OET and PET sites (Table 10).

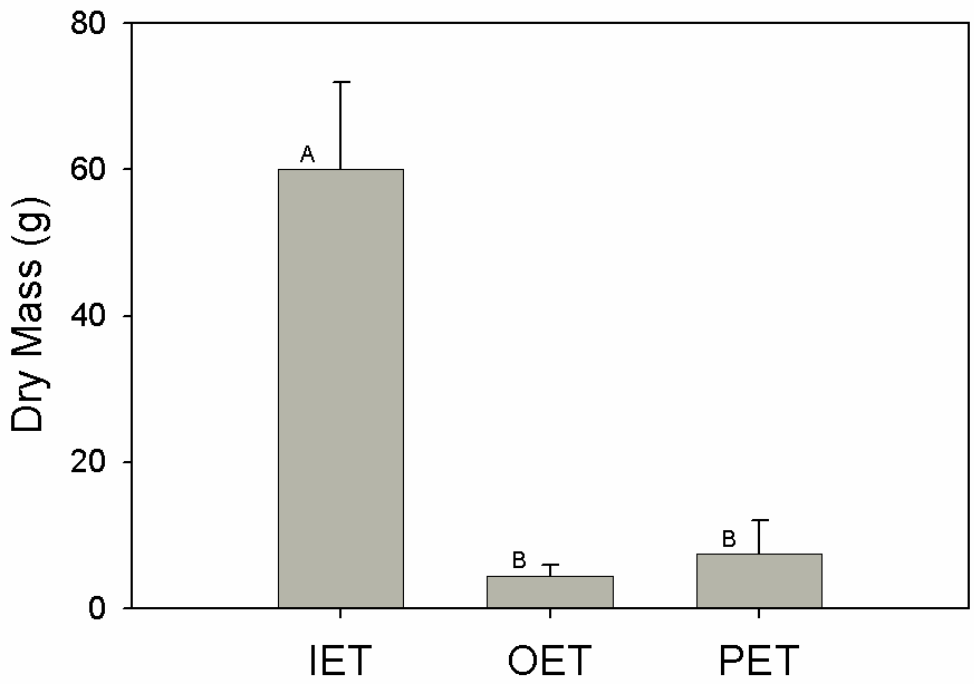

Figure 9: Macrophyte dry mass response to exclosure treatments in the high carp biomass reach of Spring Creek, UT at the end of the experiment in mid-October 2008. Bars with different letters are significantly different at the 0.05 alpha level.

Table 10: Presence-absence list of macrophyte species observed in the low carp biomass and at the inside (IET), outside (OET), and partial (PET) exclosure treatment sites opf the high carp biomass reach of Spring Creek, UT. Note: *Chara* is a macroalgae and not a vascular plant but was grouped with macrophytes due to similarity in vegetative structure. An x in the table indicates presence of a given species at the site.

	Reach			
	LCB	HCB		
Species		IET	OET	PET
Potamogeton filiformis	x	x	x	x
Elodea canadensis	x	x	x	x
Chara sp.	x	x		
Rannunculus aquatilus	x	x		
Nasturtium officinale	x	x		
Zanachelia palustris	x			
Unknown sp.	x			

Epiphyton - Epiphyton AFDM values per unit area were significantly greater in the LCB reach than in the HCB reach during late July (p-value = 0.07). Given the greater abundance of macrophytes in the LCB reach, this finding is not surprising. Epiphyton samples for spatial coverage and abundance per unit area were not collected for the HCB reach during the mid-October sample event preventing late growing season comparisons.

Samples per gram of macrophyte dry mass were collected on two sample dates; late July and mid-October. Epiphyton AFDM per gram of dried macrophyte tissue was not significantly different between the two reaches during the late July sample events (p-values = 0.95) but was significantly different during the mid-October sample event (p-value = 0.09; Figure 10). The HCB reach epiphyton AFDM values per gram of macrophyte drymass were 83% higher than those in the LCB reach during the mid-October sample event. Generally, the LCB reach had lower values of epiphyton AFDM per g drymass of macrophyte tissue compared to the HCB reach.

Statistical comparisons of chlorophyll *a* were not possible as two of the three HCB epiphyton chlorophyll *a* samples collected for spatial abundance analysis from the late July sample had invalid values (i.e., negative values). However, chlorophyll *a* mass per g of macrophyte tissue followed similar trends found for AFDM in that values were lower in the LCB reach than in the HCB reach (Tables 4 and 5). Epiphyton chlorophyll *a* mass per g drymass of macrophyte tissue did not differ in late July between the two reaches (p-value = 0.95) but was significantly different during the mid-July and mid-October sample

events (p-values = 0.02 and 0.09, respectively). Like epiphyton AFDM per g drymass of macrophyte tissue, epiphyton chlorophyll *a* mass per g drymass of macrophyte tissue was higher in the HCB reach (Figure 11).

Within the HCB reach, epiphyton AFDM per g drymass of macrophyte tissue did not differ across the three treatment types or the three sample events. No discernable pattern in epiphyton AFDM was found across exclosure treatments and time (Figure 11). Similarly, there was no significant difference in epiphyton chlorophyll *a* mass per g drymass of macrophyte tissue across the three treatments and the three sample events (Tables 7, 8, and 9).

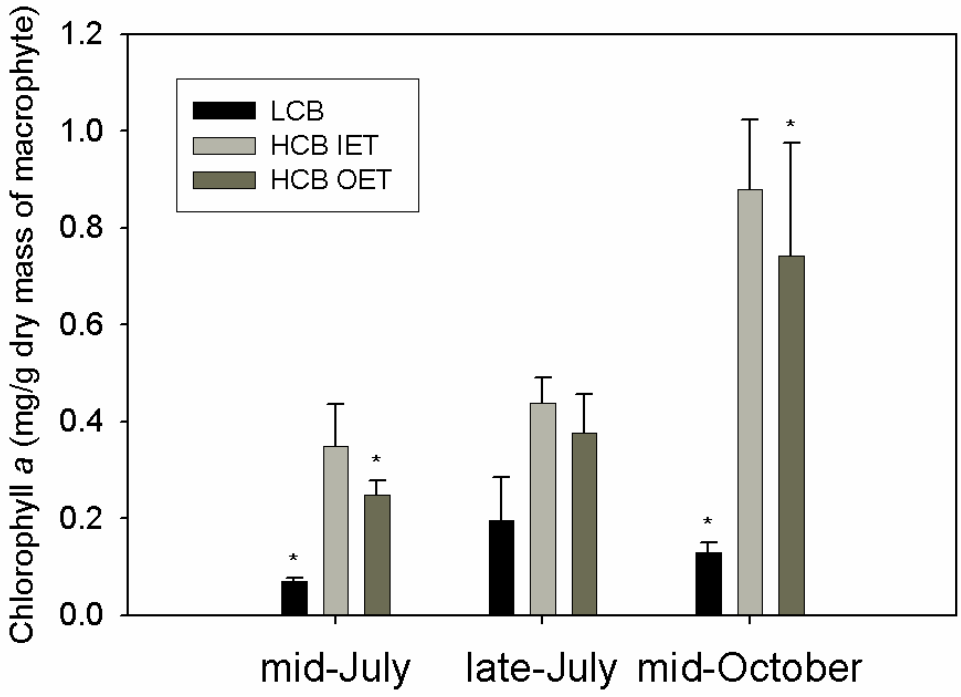

Figure 10: Epiphyton chlorophyll *a* mass per gram of macrophyte dry mass in the low carp biomass reach and at the inside (IET) and outside (OET) sites in the high carp biomass reach of Spring Creek, UT. Partial exclosure treatment sites did not differ from the IET or OET sites so were excluded from the graph. Bars with asterisks are significantly different at the 0.1 alpha level.

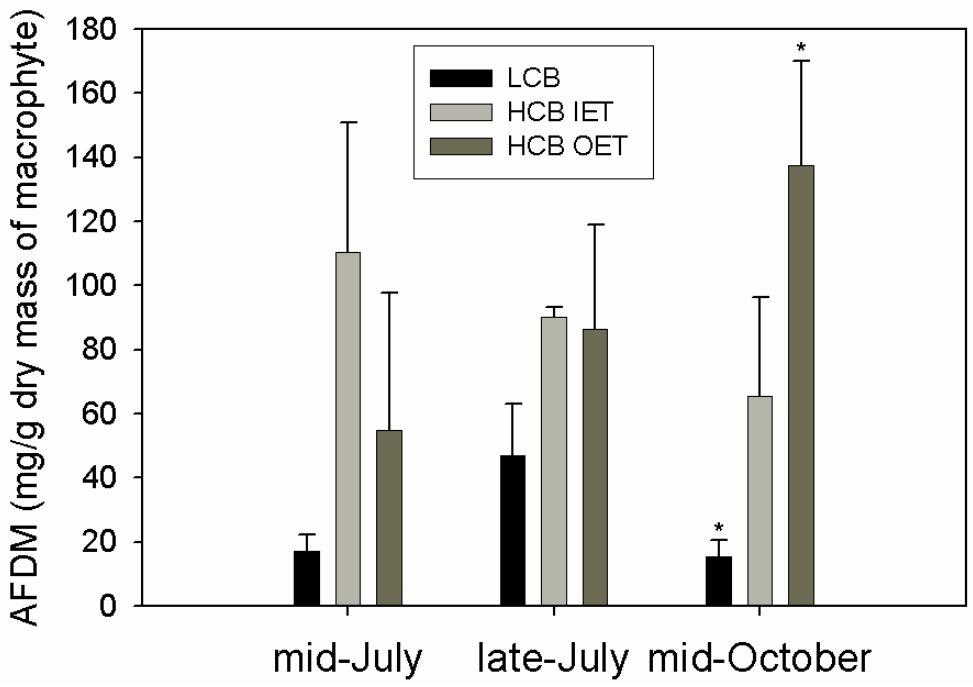

Figure 11: Epiphyton ash free dry mass per gram of dry mass of macrophyte tissue in the low carp biomass reach and at the inside (IET) and outside (OET) sites in the high carp biomass reach of Spring Creek, UT. Partial exclosure treatment sites did not differ from the IET or OET sites so were excluded from the graph. Bars with asterisks are significantly different at the 0.1 alpha level.

While not statistically different (p-value range from 0.56 – 0.71), a 50% increase in the mean epiphyton chlorophyll *a* mass per g drymass of macrophyte tissue was observed from late July to mid-October in all three exclosure treatments.

Macroinvertebrates – A significant reach by time interaction was found for macroinvertebrate biomass across the two reaches (p-value = 0.03). The interaction is characterized by increasing macroinvertebrate biomass per unit area from June to mid-October in the LCB reach and decreasing macroinvertebrate biomass per unit area from June to mid-October in the HCB reach (Figure 12).

Macroinvertebrate abundance was 135 times greater in the LCB reach in July and over 800 times greater in October than in the HCB reach (Tables 5 and 6). A total of 26 unique taxa across five functional feeding groups were identified in the LCB reach and a total of 11 unique taxa across three functional feeding groups were identified in the HCB reach (Appendix).

Within exclosure treatments in the HCB reach, the biomass of macroinvertebrates was approximately 30 times higher at the IET sites than was biomass of invertebrates at the OET or PET sites ($p = 0.0005$; Figure 13).

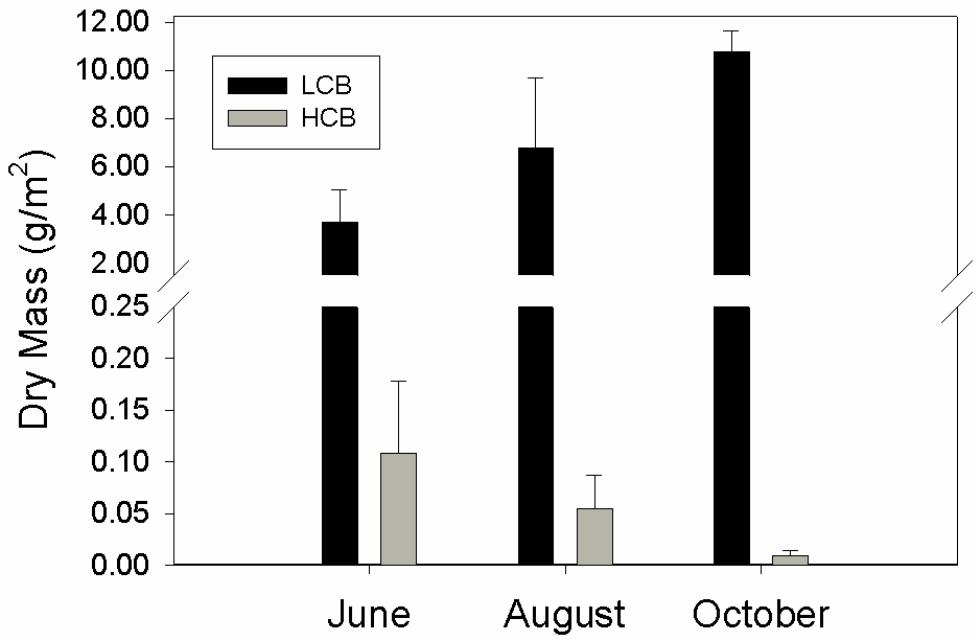

Figure 12: Macroinvertebrate dry mass in the low carp biomass and high carp biomass reaches of Spring Creek, UT across time. The data revealed a significant reach by time interaction (p-value = 0.03) hence no post-hoc comparisons were performed.

Additionally, 22 taxa were identified in the mid-October macroinvertebrate samples in the LCB reach and 18, 3, and 4 taxa for the October samples at the IET, OET, and PET sites in the HCB reach, respectively. As such, species richness was substantially higher at the IET sites than at the OET or PET sites. Four functional feeding groups; CG, predators, scrapers, and filterers were identified in the LCB reach and at the IET sites in the HCB reach in mid-October. Conversely, only one FFG, CG, was found at the OET and PET sites in the HCB reach in mid-October.

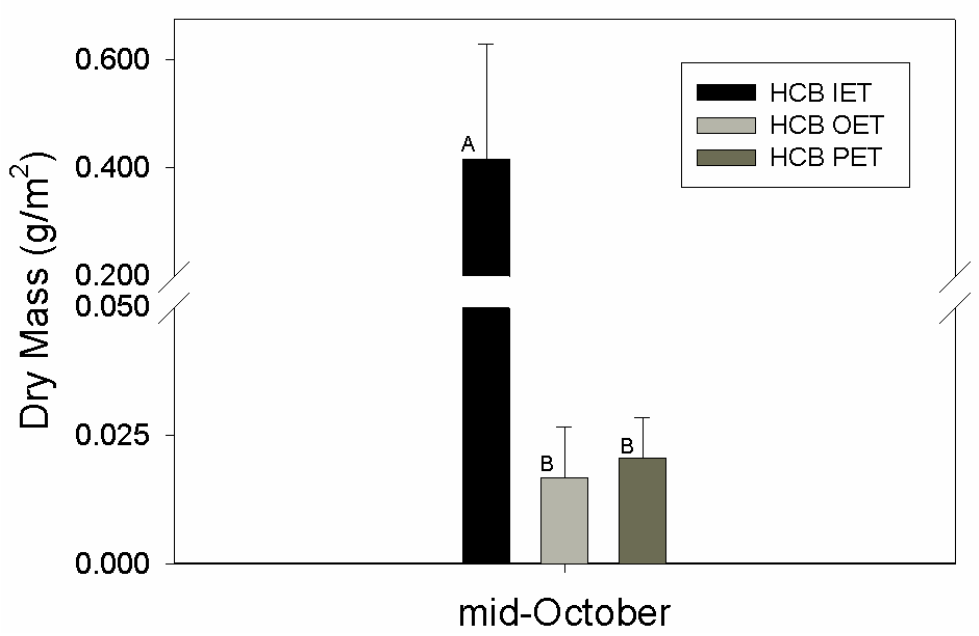

Figure 13: Macroinvertebrate dry mass response to the inside (IET), outside (OET), and partial (PET) exclosure treatments in the high carp biomass reach of Spring Creek, UT at the end of the experiment in mid-October 2008. Bars with different letters are significantly different at the 0.05 alpha level.

The Shannon-Wiener diversity index as calculated by number of individuals of each species for the LCB reach in October was 0.834, and for the

HCB reach, was 0.771, 0.393, and 0.66 for the IET, OET, and PET sites, respectively. Rank-abundance curves by number of individuals per taxa clearly show that a single taxon dominates the invertebrate community within each reach and exclosure treatment (e.g, *Hyallela* in LCB and CG chironomids at the HCB exclosure treatment sites). Furthermore, species evenness is relatively similar between the LCB and the IET sites of the HCB reach as indicated by the similar slope of the two lines (Figure 14).

The Shannon-Wiener diversity index as calculated by mass of individuals of each species for the LCB reach in October was 1.778 and for the HCB reach was 1.586, 0.298, and 0.799 for the IET, OET, and PET sites, respectively. Rank-abundance curves by mass of individual species indicate that species richness is greater when plotted by mass versus count (Figure 14). Interestingly, species evenness was higher at the IET sites for the first four most abundant species than for the four most abundant species of the LCB reach. After the sixth most abundant species, species evenness by mass is substantially higher in the LCB reach than at the IET sites of the HCB reach.

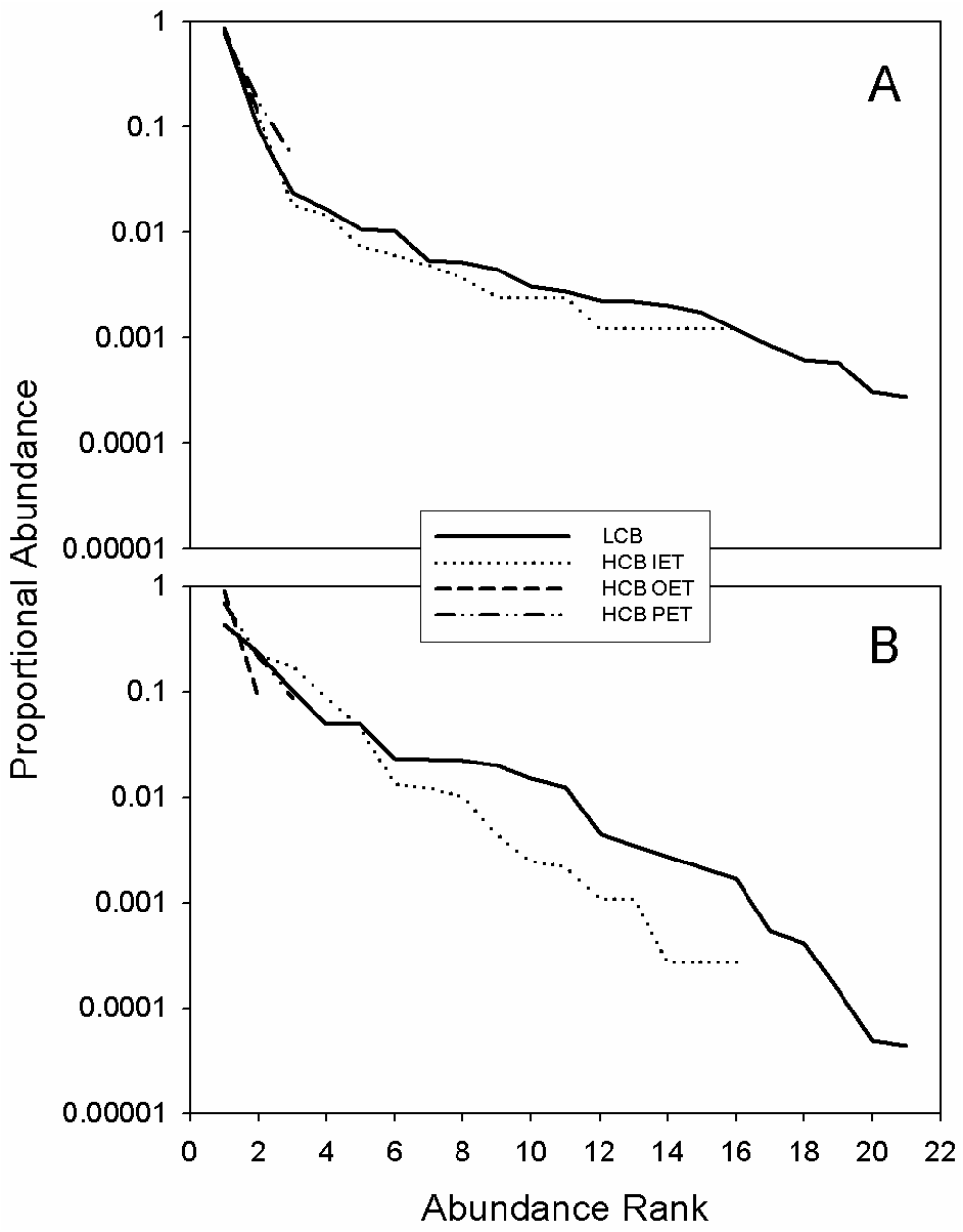

Figure 14: Rank-abundance curves for macroinvertebrate samples collected in mid-October 2008 at the low carp biomass reach and at the inside (IET), outside (OET) and partial (PET) exclosure treatment sites in the high carp biomass reach of Spring Creek, UT. Panel A is macroinvertebrate proportional abundance by count and panel B is proportional abundance by mass.

Measures of Ecosystem Function

Nitrogen Dynamics

^{15}N Tracer test - Pump rates throughout the duration of study did not deviate from the targeted rate of 10 ml/minute. Average injectate concentrations were 81.31 mg/L for the LCB reach and 90.35 mg/L for the HCB reach. A total of 7.403 grams of NH_4-^{15}N was injected into the LCB reach and a total of 8.522 grams were injected into the HCB reach.

Longitudinal patterns of bromide concentration within each reach indicated that our multiple-drip injection setup did not adequately mix the solute with stream water. As such, I did not calculate uptake lengths (sensu Newbold et al. 1981) and associated parameters from water NH_4-^{15}N concentrations. Inadequate mixing is unlikely to influence mass balance calculations negatively, as delta ^{15}N values for most compartments display expected temporal trends (see Figure 15 or 16 for example).

Isotopic composition –FBOM delta ^{15}N values showed a reverse trend in that delta ^{15}N values increased with distance downstream (Figure 15). Delta ^{15}N values at the IET sites were approximately half the value of the OET sites and up to a third of the delta ^{15}N values of the PET sites on day 24.

Macrophyte delta ^{15}N values for a given sample event in the LCB reach displayed expected patterns of longitudinal uptake in that delta ^{15}N values were highest at the 10 m sample station and declined with increasing distance downstream (Figure 16).

Conversely, macrophyte delta ^{15}N values in the HCB reach were lowest at the 15 m sample station and increased with increasing distance downstream. There were no major differences in macrophyte delta ^{15}N values across the three exclosure treatments. As expected, delta ^{15}N values of macrophytes declined following termination of the injection as a result of turnover (Figure 16).

In the LCB reach, collector/gatherer (CG) macroinvertebrate delta ^{15}N values displayed expected longitudinal patterns in that highest enrichment was at the 10 m sample location with progressive declines in enrichment downstream (Figure 17). Predator macroinvertebrate delta ^{15}N values increased dramatically from day 24 to day 84. Within the HCB reach, CG macroinvertebrate delta ^{15}N values were only marginally enriched.

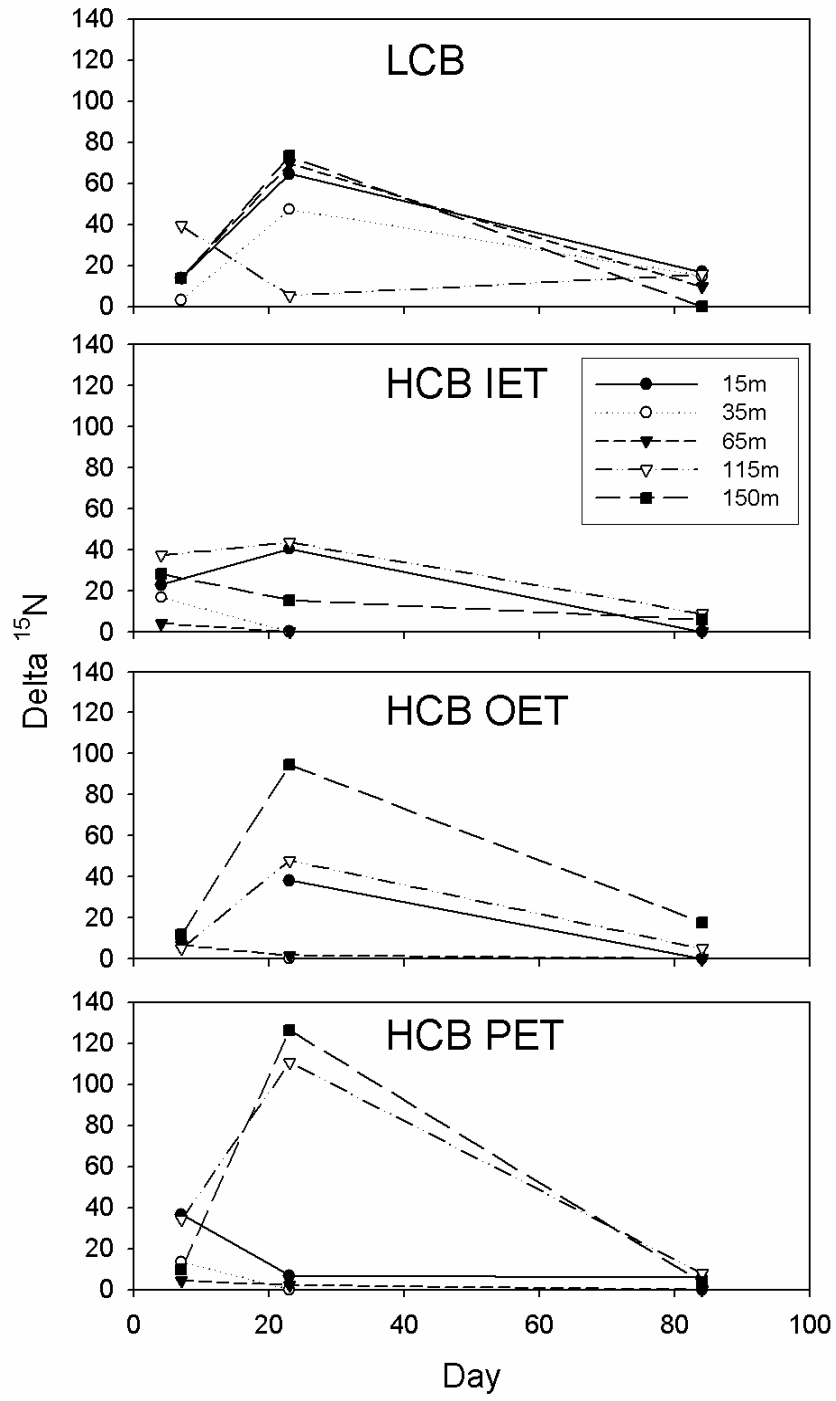

Figure 15: Delta ^{15}N values of FBOM at five sample stations in the low carp biomass reach and the inside (IET), outside (OET), and partial (PET) exclosure treatment sites across five sample stations in the high carp biomass reach of Spring Creek, UT, 2008.

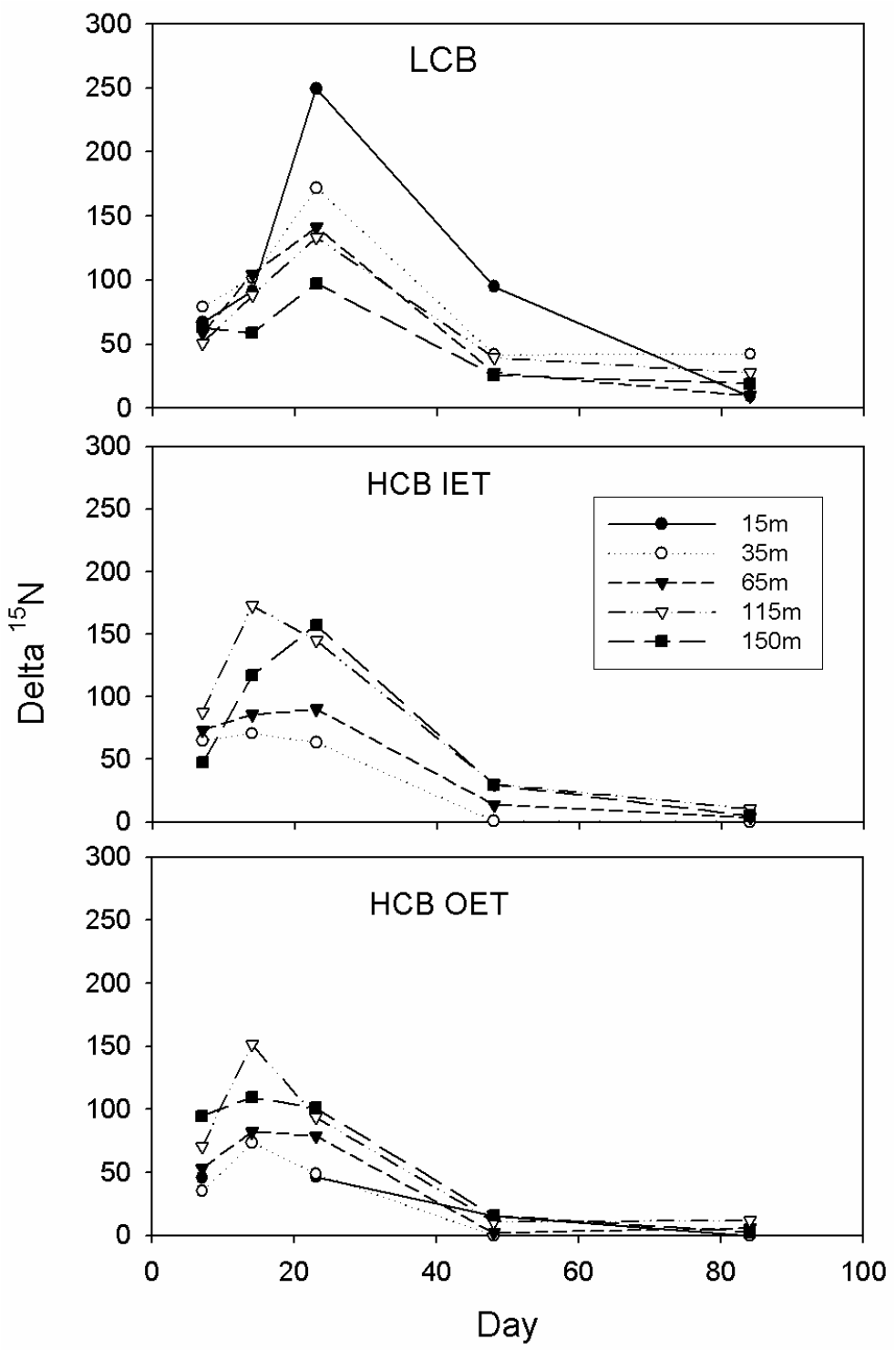

Figure 16: Delta ^{15}N values of macrophytes collected at five sample stations in the low carp biomass reach and the inside (IET), outside (OET), and partial (PET) exclosure treatment sites across five sample stations in the high carp biomass reach of Spring Creek, UT, 2008.

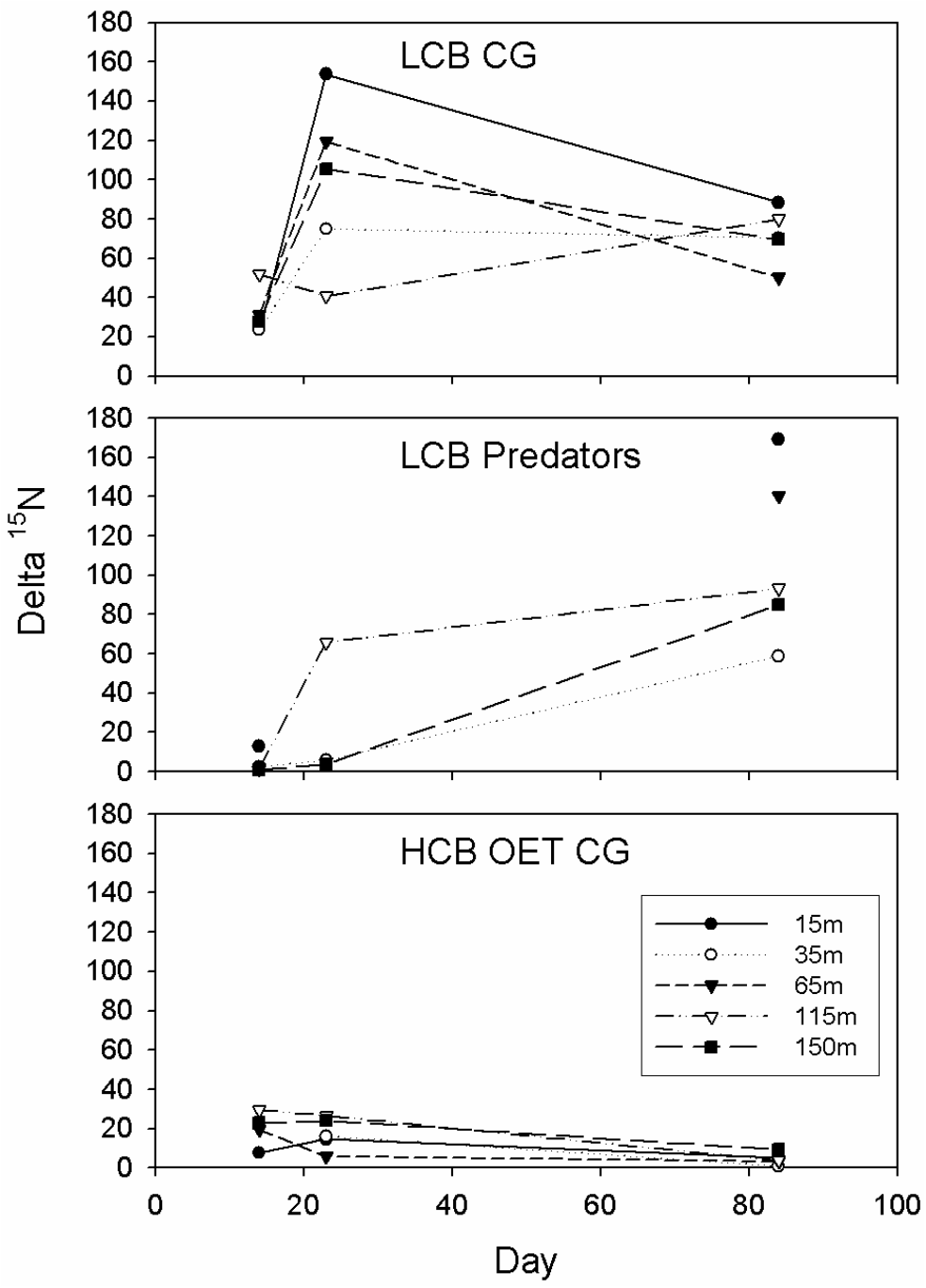

Figure 17: Delta ^{15}N values of macroinvertebrates collected at five sample stations in the low carp biomass reach and the outside (OET) exclosure treatment sites across five sample stations in the high carp biomass reach of Spring Creek, UT, 2008. CG is collector/gatherer invertebrates.

Compartment-specific uptake rates – In the absence of day 54 FBOM isotope data, I was unable to calculate NH4 turnover rates and thus NH4 uptake rates for FBOM.

Macrophyte NH_4 uptake rates were on average 120 times faster in the LCB reach than in the HCB reach. NH_4 uptake rates increased from day 7 to day 14 in both reaches but were not significantly different ($p = 0.21$). Similarly, no differences were observed among the IET, OET, and PET sites of the HCB reach ($p = 0.16$, 0.24, and 0.99, respectively; Figure 18).

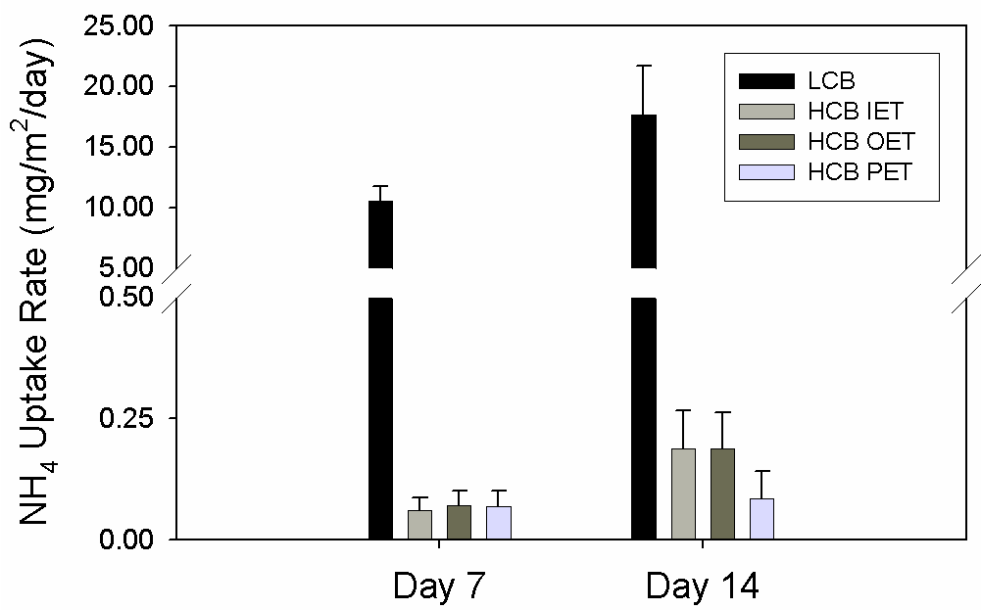

Figure 18: Macrophyte NH_4 uptake rates for days 7 and 14 of the ^{15}N injection in the low carp biomass reach and at the inside (IET), outside (OET), and partial (PET) exclosure treatment sites in the high carp biomass (HCB) reach of Spring Creek, UT, 2008.

No major differences in macrophyte NH_4 uptake rates were observed across the three exclosure treatments. NH_4 turnover rate for macrophytes was calculated to be 18.3 days for the LCB reach and 15.7 days for the HCB reach.

Floating *Cladophora* mat uptake rates were 6.7 times greater in the LCB reach than in the HCB reach (Figure 19). *Cladophora* uptake did not differ between day 7 and day 14 in the HCB reach or in the LCB reach.

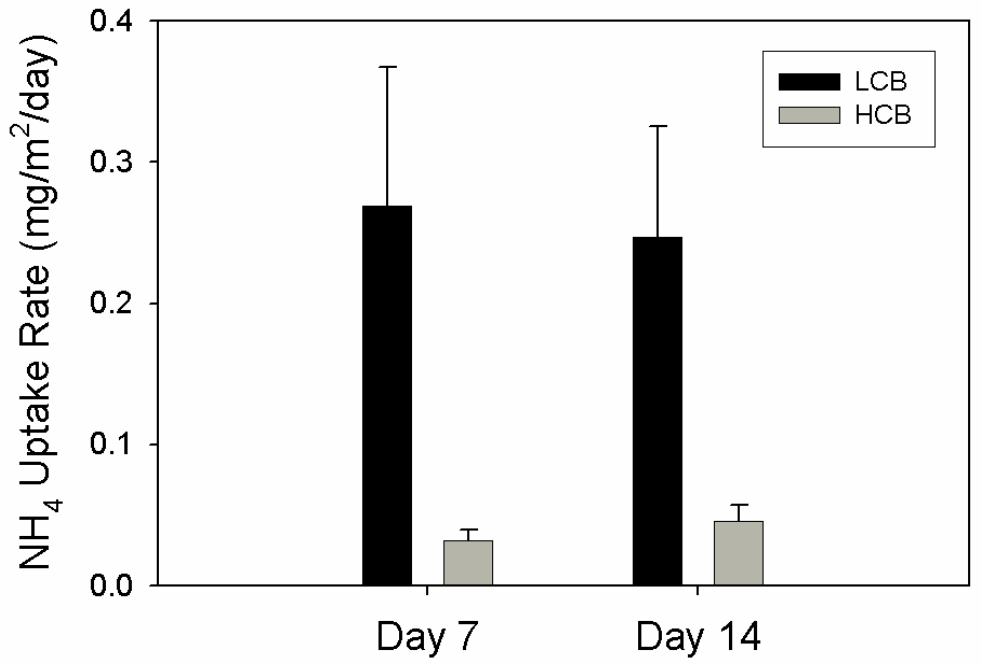

Figure 19: Cladophora NH_4 uptake rates for days 7 and 14 of the ^{15}N injection in the low carp biomass reach and at the outside (OET) exclosure treatment sites in the high carp biomass reach of Spring Creek, UT, 2008.

Nitrogen mass balance - I used the autotroph distribution survey conducted during October for the day 24 (i.e., July) mass balance, as macrophyte distribution was similar between the two months. I used *Cladophora* distribution estimates from the rapid assessment method for mass balance calculations because the distribution of *Cladophora* was predominantly along the periphery of each reach and thus the view box method provided poor estimates.

A total of 3.204 g of the injected ^{15}N was accounted for in the LCB reach and 1.712 g in the HCB reach representing 43.3% and 20.1% of the total ^{15}N injected into each reach, respectively. Within each reach, FBOM had the greatest contribution to total ^{15}N uptake with total mass of ^{15}N assimilated remarkably similar between the two reaches; 1.797 and 1.692 for the LCB and HCB reaches, respectively. However the proportional role of FBOM differed dramatically across the two reaches (Figure 20). This difference is largely driven by the assimilatory role of macrophytes in the LCB reach as they contained 36.6% of the accounted for ^{15}N (Table 11).

The LCB reach retained 1.543 g of injected ^{15}N two months after termination of the injection while the HCB reach retained only 0.253 g. These values are 48.1% and 14.8% of the ^{15}N that was retained in the LCB reach and the HCB reach at the end of the injection (i.e., day 24), respectively (Figure 21). The relatively large long-term retention found for the LCB reach was driven by FBOM - 88.3% of the accounted for ^{15}N on day 84 was in FBOM representing 75.8% retention of the ^{15}N found in FBOM on day 24 (Table 12).

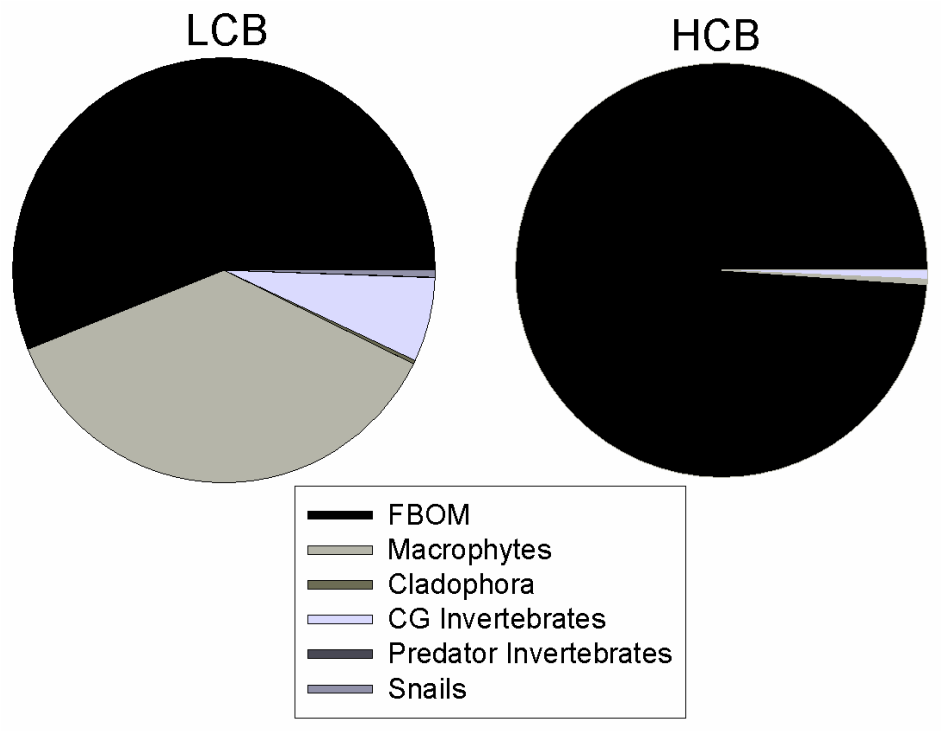

Figure 20: Proportional role of six biological compartments to NH_4-^{15}N uptake and retention on day 24 of the stable isotope injection in the low carp biomass reach (LCB) and the high carp biomass reach (HCB) of Spring Creek, UT, 2008. CG invertebrates are collector/gatherer macroinvertebrates.

Table 11: ^{15}N mass balance for day 24 of the NH_4-^{15}N injection in the low carp biomass and high carp biomass reaches of Spring Creek, UT, 2008.

	LCB		HCB	
Biological Compartment	Total 15N (g)	% of Total accounted for ^{15}N	Total 15N (g)	% of Total accounted for ^{15}N
FBOM	1.797	56.08	1.692	98.88
Macrophytes	1.174	36.64	0.00646	0.38
Cladophora	0.00888	0.28	0.00094	0.05
CG Invertebrates	0.206	6.41	0.0118	0.69
Predator Invertebrates	0.00088	0.03	0	0.00
Gastropods	0.0178	0.56	0	0.00
Total	3.204		1.712	

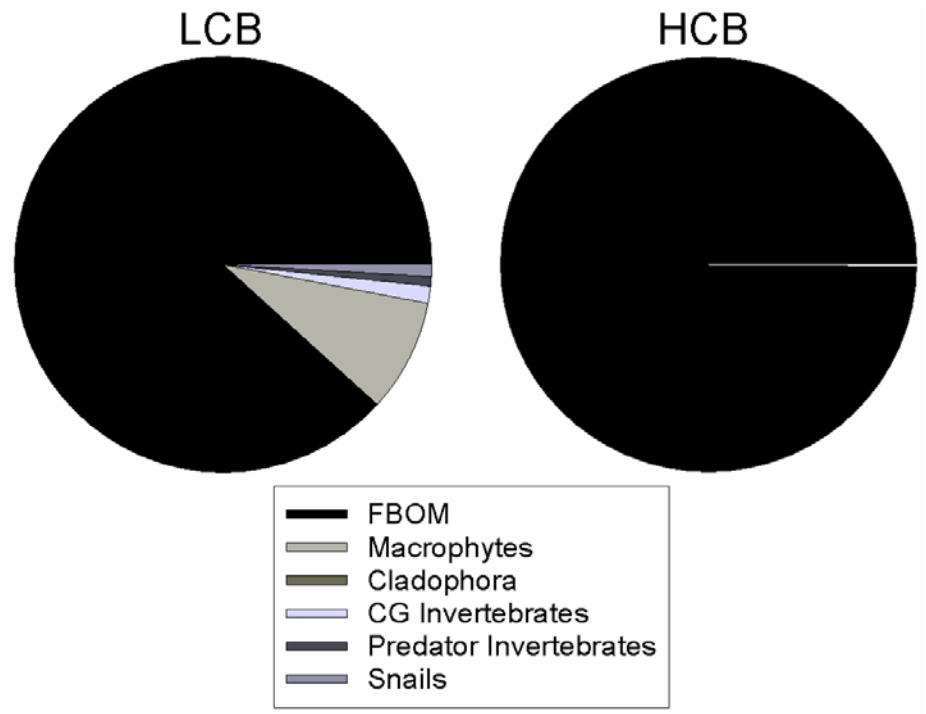

Figure 21: Proportional role of six biological compartments to NH_4-^{15}N uptake and retention on day 24 of the stable isotope injection in the low carp biomass reach (LCB) and the high carp biomass reach (HCB) of Spring Creek, UT, 2008. CG invertebrates are collector/gatherer macroinvertebrates.

While the delta ^{15}N value/ml of FBOM decreased from day 24 to day 84 in FBOM in the LCB reach, the total N concentration/ml of FBOM nearly doubled over this time period.

Two months after termination of the injection, macrophytes and CG invertebrates in the LCB reach retained ~10% of the ^{15}N that they had assimilated by day 24 while snails retained 80%. Predator invertebrates had a 13 fold increase in ^{15}N mass from day 24 to day 84 in the LCB reach (Figure 22). By day 84, macrophytes within the HCB reach retained ~2% of the ^{15}N that they had assimilated by day 24 and macroinvertebrates retained only 0.002%.

Table 12: ^{15}N mass balance for day 84 of the NH_4-^{15}N injection in the low carp biomass and high carp biomass reaches of Spring Creek, UT, 2008.

	LCB			HCB		
Biological Compartment	Total ^{15}N (g)	% of Total accounted for ^{15}N	% of day 24	Total ^{15}N (g)	% of Total accounted for ^{15}N	% of day 24
FBOM	1.361	88.25	75.8	0.253	99.9	15
Macrophytes	0.135	8.75	11.5	0.0001	0.053	2.1
Cladophora	0.00001	0.00	0.1	0.000003	0.001	0.35
CG Invertebrates	0.021	1.33	10	0.000003	0.001	0.002
Predator Invertebrates	0.012	0.74	1301	0	0	-
Gastropods	0.014	0.93	80.2	0	0	-
Total	1.543		48.1	0.253		14.8

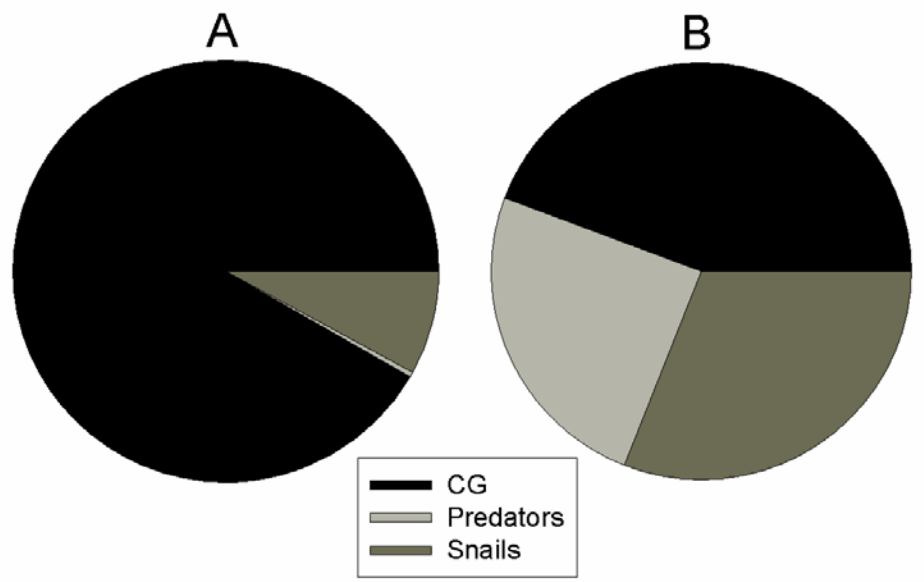

Figure 22: Proportional role of three macroinvertebrate functional feeding groups to ^{15}N retention on day 24 (A) and day 84 (B) of the study in the low carp biomass reach of Spring Creek, UT, 2008.

Ecosystem Metabolism

Rates of GPP exceeded rates of CR for all nine days that the sondes were deployed in the LCB reach. Conversely, rates of GPP exceeded rates of CR on only four of the nine days in the HCB reach. As such, the average P:R value for the LCB reach was 1.2 and was 0.99 for the HCB reach (Table 12). Differences in P:R values between the two reaches were statistically significant ($p = 0.0001$). Rates of GPP and NEM were significantly different between the two reaches ($p = 0.003$ and 0.0001, respectively) with rates of GPP in the LCB reach 18.2% higher than in the HCB reach (Figure 23). No significant difference in rates of community respiration were found between the two reaches ($p = 0.82$).

Table 13: Rates of ecosystem metabolism measured across nine days in late July 2008 in the low carp biomass and high carp biomass study reaches of Spring Creek, UT. Data are means ± SE. GPP is gross primary production, CR is community respiration, NEM is net ecosystem metabolism, and P/R is the ratio between GPP and CR.

Reach	GPP	CR	NEM	P/R
LCB	15.49 ± 0.44	12.82 ± 0.23	2.67 ± 0.26	1.21 ± 0.02
HCB	12.67 ± 2.017	12.68 ± 0.54	-0.01 ± 0.18	0.996 ± 0.013

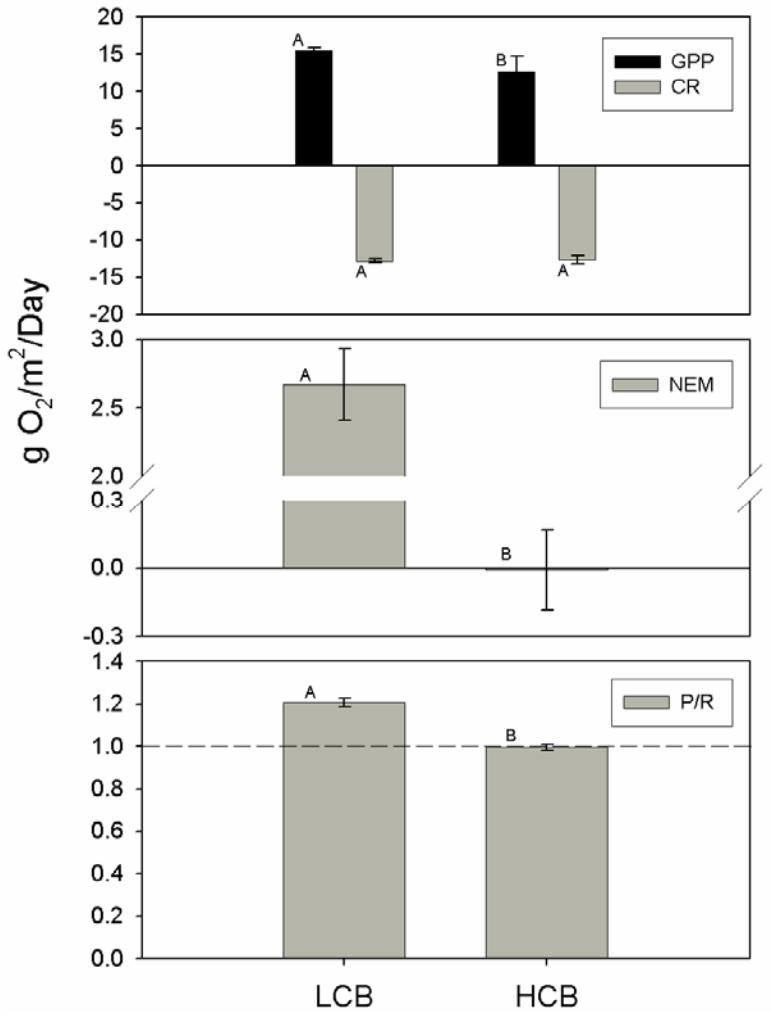

Figure 23: Ecosystem metabolism parameters calculated from O_2 mass balance measured continuously for nine days in late July 2008 in the low carp biomass and high carp biomass study reaches of Spring Creek, UT. Dashed line indicates P/R value of 1.0. Data are means ± SE. Bars with different letters are significantly different at the 0.05 alpha level.

DISCUSSION

Measures of Ecosystem Structure

Physicochemical Parameters

I found significant differences in physical characteristics between the two study reaches. However, differences between the two reaches are expected to have opposite affects on nutrient dynamics. For example, the wider shallower channel of the HCB reach would be expected to promote greater uptake rates than would the narrower, deeper channel of the LCB reach due to increased contact between the water and benthos and greater benthic surface area (Alexander et al. 2000; Peterson et al. 2001). The increased water - benthic contact of small, low order streams along with their sheer abundance relative to higher order streams contributes to their disproportionate role in nutrient uptake (Peterson et al. 2001). Further, the ambient nutrient chemistry was higher in the LCB reach than in the HCB reach, which may also promote lower uptake rates (Webster et al. 2003). With this in mind, the results of our tracer test are likely to be conservative.

Biological Compartments

Carp biomass – The distribution of stream fishes is heterogeneous across the landscape (Fausch et al. 2002) and often coincides with the patchy distribution of the physical habitats necessary to support various lifestages (Schlosser 1991). This heterogeneity may be viewed as creating hotspots or areas of high density of species or specific lifestages. With that said, the

disparate distribution of carp within Spring Creek may reflect the spatial distribution of physical habitats within the network. Specifically, the high carp densities found in the HCB reach may be partially driven by the presence of and access to adjacent man-made ponds. While I did not track individual movement patterns of carp, I observed carp moving freely between the creek and one of the two ponds adjacent to the HCB reach throughout the summer. Movement between the stream and this pond suggests that these ponds are utilized in conjunction with the stream as summer habitat. My observations are consistent with research in the Murray-Darling Basin of Australia that highlight the importance of off channel and floodplain habitats in supporting carp populations (Driver et al. 2005; Stuart and Jones 2006). Furthermore, several authors have highlighted the importance of lateral habitats in subsidizing stream ecosystem engineers (Flecker 1996; Flecker and Taylor 2004; Moore 2006) which suggests habitat subsidies may be a common attribute that sustains high densities of ecosystem engineers in streams (Moore 2006).

The biomass estimates of carp in Spring Creek fall within the “high” and well below the “low” ranges reported for experimental studies of carp biomass effects on aquatic ecosystems. These densities range from 476 – 670 kg/ha for high densities and 174 – 330 kg/ha for low densities (Parkos et al. 2003; Chumchal and Drenner 2004; Driver et al. 2005). Driver et al. (2005) suggest that a carp density of 400 kg/ha or greater is needed to elicit a carp mediated response in water quality; substantially less (260 kg/ha) is sufficient to modify habitat (Sidorkewicj et al. 1998). Thus, carp densities found in the HCB reach

have been shown to be sufficient in instigating deleterious responses in lentic ecosystems.

Spatial autotroph distribution – Given the exclosure treatment responses in the HCB reach, differences in macrophyte spatial distribution between the two reaches is mediated by carp engineering. This result is consistent with work by Sidorkewicj et al. (1998) who found carp dentisties of 260 kg/ha were sufficient to significantly reduce or eliminate aquatic macrophytes in Argentine irrigation canals; the loss of aquatic macrophytes is frequently cited as the single greatest effect of carp on lentic ecosystems (Roberts et al. 1995; Parkos et al. 2003; Matsuzaki et al. 2007). This concurs with results found for lentic ecosystems (Threinen and Helm 1954; Roberts et al. 1995; Williams et al. 2002; Parkos et al. 2003; Matsuzaki et al. 2007) and suggests high carp biomass effects on macrophytes are consistent across lentic and lotic ecosystems.

Fine benthic organic matter - The contribution of macrophytes and their associated epiphytes to nutrient uptake in lakes (Carpenter and Lodge 1986; Madsen and Cedergreen 2002; Caraco et al. 2006) and primary production in both lakes and streams (Carpenter and Lodge 1986; Kaenel et al. 2000; Caraco et al. 2006) is well recognized. Therefore, in the absence of macrophytes, I expected to find an increase in episammon abundance in response to increased limiting resources (e.g., light and nutrients). Contrary to this expectation, no compensatory response of FBOM, measured as AFDM or chlorophyll *a* concentration, was observed in the HCB reach. No difference in AFDM and chlorophyll *a* among exclosure treatments suggests that carp disturbance

frequency is not the mechanism driving episammon abundance in the HCB reach. Furthermore, failure to detect a difference between the two reaches suggests neither light nor nutrients is limiting episammon abundance in the LCB reach. In a review of post-disturbance periphyton recovery, Steinman and McIntire (1990) conclude that small, homogeneous substrates such as silt support less periphyton than does larger and more heterogeneous substrates such as cobble. With this in mind, substrate within both the LCB and HCB reaches is homogenous and dominated by small (<2mm in diameter) particles (personal observation). This suggests that although light availability and nutrient concentrations are high in the HCB reach, substrate size may limit periphyton production.

Macrophyte and floating Cladophora mats - The large response of macrophytes to carp exclosure highlights the relatively rapid recovery ability of Spring Creek to carp exclusion/removal. The recovery and resilience of lotic systems has been linked to the spatial distribution of refugia within a network (Sedell et al. 1990; Niemi et al. 1990). The close proximity of the HCB reach to an upstream refuge reach (e.g., the LCB reach) is likely responsible for the observed rapid recovery in the spatial distribution and total biomass of macrophytes at the IET sites. The interaction between engineered and non-engineered patch-scale species richness (Gutierrez et al. 2003; Wright et al. 2006; this study) provides evidence that ecosystem engineers can modulate the presence and distribution of refugia within stream networks.

The response of individual species at the IET sites is likely driven by dependent factors such as dispersal ability and generation time (sensu Niemi et al. 1990). Colonization of five of the seven species observed in the LCB reach at the IET sites during the course of this study suggests that these factors act on a short temporal scale of weeks to months.

Epiphyton – Differences in epiphyton abundance per gram of macrophyte dry mass is difficult to ascertain given my study design. For example, in lentic ecosystems, nutrient excretion by benthivorous fish has been shown to increase dissolved nutrient concentrations which has been linked to increased epiphyton abundance (Williams et al. 2002; Matsuzaki et al. 2007). However, given the lower nutrient concentrations in the HCB reach, increased nutrient concentrations due to carp excretion is not a likely explanation for the observed epiphyton differences documented in this study.

Several studies have highlighted the symbiotic relationship between snails and macrophytes as important drivers of epiphyton abundance (Underwood et al. 1992; see also Carpenter and Lodge 1986 and Bronmark and Vermaat 1998). For example, in an experimental study, Underwood et al. (1992) found that epiphyton abundance and composition was significantly reduced by snail grazer activity and, consequently, measures of individual macrophyte growth were increased. By reducing epiphyton abundance, individual macrophyte growth and persistence is improved which subsequently increases critical habitat for snails (Underwood et al. 1992). Given the absence of scraper snails in the OET sites and the relatively high abundance of scraper snails in the LCB reach in mid-

October, the greater epiphyton AFDM and chlorophyll *a* at the OET sites in mid-October may be due to differences in the biomass of scraper snails.

Macroinvertebrates - Differences in macroinvertebrate abundance and community assemblage between the two reaches appear to be mediated by carp induced macrophyte reduction. As noted by Parkos et al. (2003), the extent to which carp will mediate macroinvertebrate assemblages will correspond to the extent to which carp reduce macrophyte abundance. Carp-induced loss of macrophyte biomass at the reach scale in essence can be viewed as a simplification of macroinvertebrate habitat which ultimately limits macroinvertebrate biomass and species richness. Crooks (2002) suggested that when ecosystem engineers reduce habitat complexity within engineered patches species richness will decline. Data presented here support this hypothesis as macroinvertebrate species richness was severely diminished within the carp engineered HCB reach.

At larger spatial scales, however, the patch-specific effects of ecosystem engineers have been shown to increase habitat heterogeneity and thus to increase species diversity (Vander Zanden 1999; Crooks 2002; Wright et al. 2006). With this in mind, it is conceivable that the heterogeneous distribution of carp throughout Spring Creek may enhance macroinvertebrate diversity by creating a mosaic of macrophyte and sediment dominated patches. To explore this possibility, I pooled the invertebrate samples of the LCB reach with the OET sites of the HCB reach and found only a marginally higher Shannon-Wiener diversity index score (0.844) compared to the value found for the LCB reach

alone (0.834). Furthermore, the rank-abundance curve of the pooled data was essentially identical to that of the LCB reach alone indicating that pooling the two reaches did not result in an increase in macroinvertebrate evenness (Figure 24). Although this analysis is limited by replication (only one reach or "patch" of engineered and non-engineered habitat was tested) results from published studies support the conclusion that macroinvertebrate communities are severely depauperate in carp engineered habitats (Parkos et al. 2003; Miller and Crowl 2006).

The biomass and diversity response of invertebrates to carp exclosure was astonishing and indicates that the macroinvertebrate community of Spring Creek is capable of rapid re-colonization when carp are excluded and habitat restored (i.e., macrophyte beds restored). As mentioned for macrophytes, the recovery/re-colonization rate of the invertebrate community is likely driven by the relative close proximity of the HCB reach to the "refuge" LCB reach (Niemi et al. 1990; Sedell et al. 1990). While species richness and evenness were remarkably similar for the LCB reach and the IET sites, the rank abundance of taxa differed between the two reaches. For example, when species richness was assessed by number, chironomids were the dominant taxa within the IET sites followed by *Hyallela* and *Baetis* while *Hyallela*, Caecidotea and Physidae snails were the dominant taxa in the LCB reach. Differences in dominant taxa may be due to intraspecific time lags of a species' ability to recolonize disturbed patches (Leibold et al. 1997). As such, the response of species richness to driving factors

may function on longer temporal scales than those typical of experimental manipulations (Leibold et al. 1997; Dodson et al. 2000).

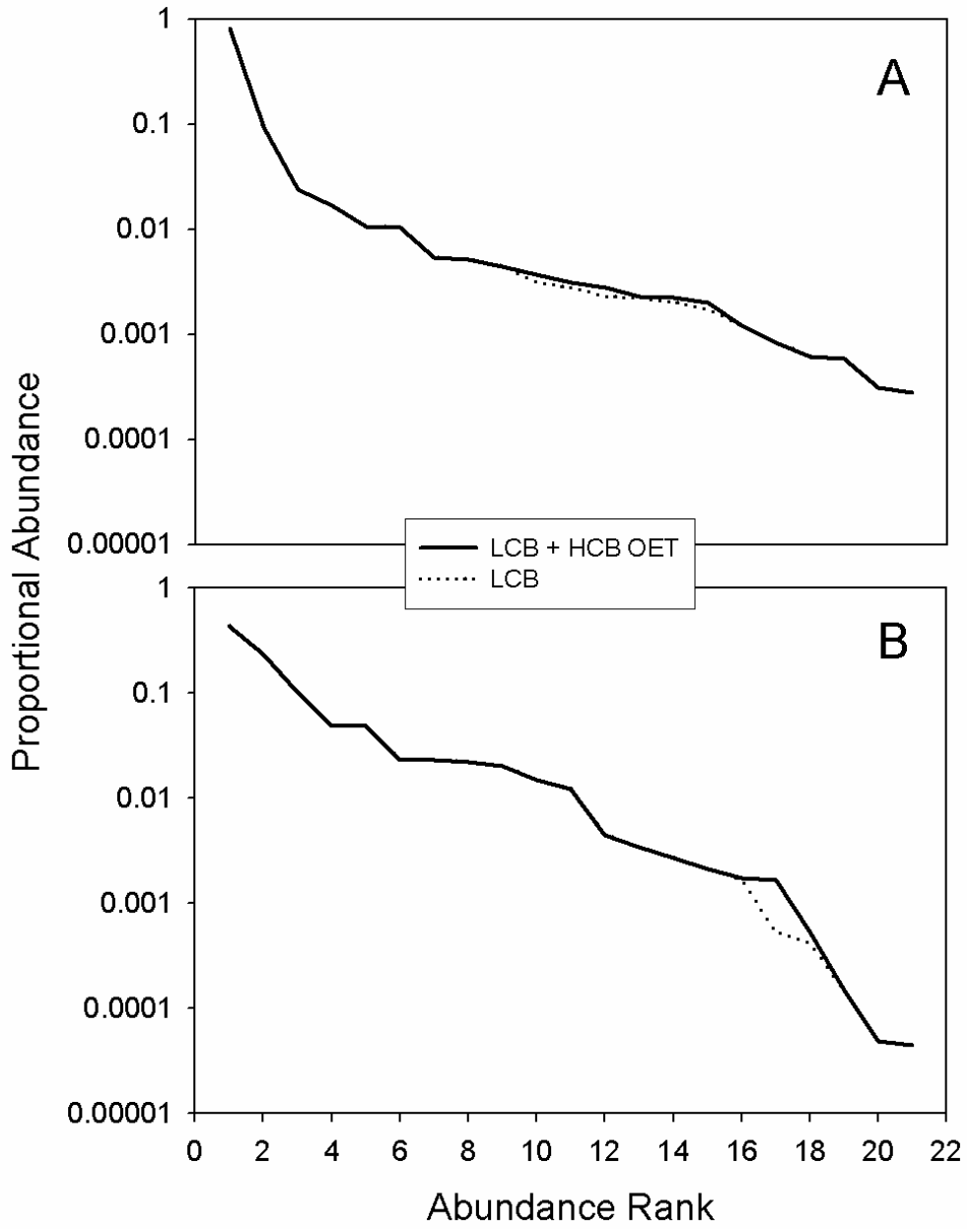

Figure 24: Pooled (low carp biomass reach (LCB) plus outside (OET) exclosure treatment sites in the high carp biomass reach (HCB); Panel A) vs. low carp biomass reach (LCB) samples by themselves macroinvertebrate rank-abundance curves for mid-October 2008. Panel A is macroinvertebrate proportional abundance by count and panel B is proportional abundance by mass.

Measures of Ecosystem Function

Nitrogen Dynamics

Compartment-specific uptake rates – In general, higher macrophyte and *Cladophora* uptake rates in the LCB reach reflect the large differences in macrophyte and *Cladophora* biomass between the two reaches and thus results in the large role of macrophyte assimilation in NH_4 uptake in the LCB reach. Increasing trends in uptake rates throughout the duration of the injection is probably due the fact that I attributed the change in delta ^{15}N values within autotroph pools entirely to assimilation of NH_4-^{15}N and did not consider mineralization and assimilation of NO_3-^{15}N.

Nitrogen mass balance – As ecosystem engineers (Caraco et al. 2006), it is not surprising that macrophyte reduction had far reaching implications on ecosystem structure and function. While many studies have addressed the role of macrophytes in aquatic ecosystems, to my knowledge, this study represents the first exploration of the consequences of macrophyte reduction on nitrogen dynamics in a lotic ecosystem.

Macrophytes were a dominant source of NH_4-^{15}N uptake within the LCB reach which suggests the assimilatory role of macrophytes play an important role in the nitrogen cycle within non-carp engineered patches. Macrophyte assimilation of dissolved NH_4 has several important implications for stream nitrogen dynamics. First, this finding clearly underscores the fact that macrophytes can and do play an important role in nitrogen uptake from the water column (Madsen and Cedergreen 2002) and thus can be important drivers of

water quality in streams. Second, the longer generation time of macrophytes relative to other autotrophs (e.g., periphyton) and heterotrophic microbes infers an inherently longer retention time of assimilated nutrients within autotroph biomass (Carpenter and Lodge 1989) and thus increased opportunity for trophic transfer via herbivory. Additionally, macrophyte stands provide critical habitat for macroinvertebrates and thus promote a more diverse and abundant invertebrate community (this study; Parkos et al. 2003; Miller and Crowl 2006). As such, macrophytes facilitate trophic transfer of nitrogen to both primary consumers and primary predators by supporting a functionally more diverse invertebrate community. For example, scrapers, such as snails, and predatory invertebrates were only found at locations dominated by macrophytes (i.e., in the LCB reach and at the IET sites in the HCB reach).

Due to low abundance, I was only able to collect macroinvertebrates for ^{15}N tissue analysis at a few exclosure sites by sieving leftover FBOM samples in the HCB reach. Additionally, Corixids, which were the only invertebrates I was able to consistently collect, were only found along the channel margin (they prefer low velocity peripheral habitats and thus were not present at exclosure sites). Habitat preference and high mobility precluded the collection of Corixids during the biomass sampling which was performed with a surber sampler. As such, the biomass abundance estimates were derived from “open” channel taxa such as chironomids and the ^{15}N tissue analysis were derived from Corixids. Thus, the piecemeal nature of the macroinvertebrate ^{15}N data for the HCB reach hinders the strength of interpretation of the data.

The macrophyte mediated difference in macroinvertebrate biomass and community assemblage between the two reaches had a pronounced influence on trophic transfer of nitrogen within each reach. The more diverse invertebrate community, both in terms of species richness and FFG, of the LCB reach, in part, facilitated greater long-term retention of assimilated nitrogen. For example, while collector-gatherer invertebrates retained 91.7% of the total ^{15}N assimilated by invertebrates on day 24 in the LCB reach, their contribution to invertebrate retention on day 84 was only 44.3 %. The thirteen fold increase in predatory invertebrate ^{15}N retention along with the high retention rate of ^{15}N in snails (80.2%) resulted in their retention of 55.7% of the ^{15}N in macroinvertebrate tissue on day 84 in the LCB reach. This suggests that the functionally more complex and diverse invertebrate community of the LCB reach facilitated greater long-term retention of nitrogen within macroinvertebrate biomass even though overall, macroinvertebrate assimilation played a relatively benign role (i.e., ~1% of total ^{15}N accounted for on day 84) in long-term N retention when compared to other compartments (e.g., FBOM and macrophytes) in the LCB reach.

With that said, assimilation of N by macroinvertebrates has been shown to be a minor component in the role of macroinvertebrates in stream N dynamics. For example, Grimm (1988) developed a model for macroinvertebrate N dynamics in a desert southwest stream and found that while assimilation of ingested N was low, egestion of N in feces accounted for 42-64% of ingested N. Furthermore, macroinvertebrates were capable of ingesting 131% of the entire N pool underscoring the significant contribution of invertebrate egestion to

particulate organic matter standing stocks (Grimm 1988). With this in mind, the large difference in FBOM ^{15}N retention observed between the LCB and HCB reaches may be, in part, due to egestion of nutrient rich fecal material by the relatively high biomass of macroinvertebrates found in the LCB reach.

Reduction of macrophytes via carp engineering in the HCB reach instigated a cascading effect through the ecosystem that ultimately had ramifications on N dynamics. The most obvious impact of macrophyte reduction on N dynamics is loss of macrophyte assimilation of NH_4. However, loss of the indirect role of macrophytes on stream N dynamics may elicit larger quantitative effects on long-term N retention. For example, two conspicuous features of macrophyte beds is their high retention capacity of particulate matter and the nutrient rich sediments that underlie them (Sand-Jensen 1998; Schulz et al. 2003). Additionally, macrophyte retention of particulate organic matter (POM) has been implicated as a major nutrient retention mechanism in several stream networks (Svendsen and Kronvang 1993; Kronvang et al. 1999; Schulz et al. 2003). As such, the dramatic difference in long-term ^{15}N retention in FBOM within the LCB and HCB reaches is probably driven by the high retention capacity of macrophyte beds (Sand-Jensen 1998; Koester and McArthur 2000; Schulz et al. 2003) coupled with in situ production of POM in the LCB reach: macroinvertebrate egestion and non-predatory mortality (Grimm 1988) and senesced epiphyton and macrophyte tissue. Regardless of the specific source or mechanism resulting in increased^{15}N retention in the LCB FBOM, the indirect

effects of macrophytes on POM retention is an integral component of long-term N retention within non-carp engineered patches in Spring Creek.

Entrainment of POM after macrophyte senescence can result in pulses of POM and associated N downstream (Svendsen and Kronvang 1993; Kronvang et al. 1999). However, Schulz et al. (2003) found deep deposits of organic sediment layers that resembled surface sediments layers in macrophyte beds indicating that some retention occurs across years despite annual macrophyte senescence. While I did not quantify sediment volume in the two study reaches, personal observations concur with Schulz et al. (2003) in that deep and wide spread sediment deposits in the LCB reach suggests a portion of the macrophyte trapped POM is retained across seasons and years. This is further supported by the HCB reach containing only shallow and sporadically distributed sediment deposits.

Failure to detect a difference in FBOM ^{15}N retention across the three exclosure treatment sites even though macrophyte biomass response was significantly higher at the IET sites is most likely due to the spatio-temporal scale of the experiment. Specifically, the 1 m^2 exclosures limited the size of macrophyte beds to 1 m^2. As such, the exclosure size used in my experiment may have prevented establishment of a macrophyte bed sufficient in size to reduce near-bed velocities and thus to allow for particle retention.

Ecosystem Metabolism

The documented shift from an autotrophic to a more “balanced” ecosystem (i.e., an ecosystem where GPP and CR are approximately equal) in the presence of high carp biomass represents a fundamental alteration of ecosystem function. The dramatic difference in macrophyte abundance between the two reaches is the most obvious explanation for the significant reduction in ecosystem metabolism. However, Kaenel et al. (2000) found that removal of macrophytes from stream reaches within two separate systems either failed to reduce GPP or only marginally did so. To explain the weak coupling of GPP to macrophyte biomass, Kaenel et al. (2000) attributed benthic algae and its apparent rapid response to macrophyte removal as the mechanism driving observed patterns in GPP after macrophyte removal within the two streams. Because we failed to detect a compensatory response in episammon to reduced macrophyte abundance, and that macrophyte abundance was significantly higher at the IET sites than at the OET and PET sites, the reduction in GPP, NEM, and P:R within the HCB reach can be directly attributed to carp engineering. This indicates that when periphyton production is limited by substrate size and where allochthonous inputs are minimal, macrophytes and their associated epiphyton will be the dominant energy source for the food web (Odum 1956).

Context-Dependency of Benthivorous Fish as Ecosystem Engineers

The strong responses of Spring Creek to carp engineering may be the result of an ecosystem engineer (i.e., carp) affecting another ecosystem engineer (i.e., macrophytes). Carp engineering effects in non-macrophyte dominated streams may not result in as strong of responses as those observed in Spring Creek. As such, the context-dependency of carp engineering should be explored so as to identify those ecosystems most susceptible to carp engineering. Understanding the context-dependency of carp engineering will allow for prioritization of stream ecosystems where carp control will be most beneficial (Parkos et al. 2003; Moore 2006). While I suspect the effects of carp on stream ecosystems will be, in part, context-dependent, consistent patterns in the effects benthivorous ecosystem engineers on macroinvertebrate diversity and biogeochemical cycling are evident. For example, research on the ecological role of *Prochilodus mariae*, a tropical detritivorous fish, has shown that their presence in stream reaches reduces macroinvertebrate density (Flecker 1996) and reduces NH_4 uptake rates and N and carbon retention (Taylor 2005; Taylor et al. 2006). The remarkable similarities between the ecological role of carp and *Prochilodus*, two benthivorous fishes occupying dramatically different ecosystems (i.e., temperate vs. tropical streams) suggestss that the effects of benthivorous fishes may be consistent and, therefore, predictable across diverse stream ecosystems.

CONCLUSIONS

The importance of nutrient uptake and retention in streams in regulating the downstream transport of nutrients is well recognized (Peterson et al. 2001) and is a critical ecosystem service. As such, understanding the mechanisms driving nutrient uptake and retention in streams is paramount not only to the advancement of stream biogeochemistry but also in promoting effective management and restoration of water quality and biological communities in streams. Integrating the concepts of ecosystem engineers, which has provided ecosystem ecologists with a unified theorem and cohesive framework through which scientists can link biological organisms to ecosystem processes (Jones et al. 1997), with stable isotope tracer tests may prove to be a powerful tool in stream ecology. For example, recognition of carp as an ecosystem engineer capable of dramatically reducing nitrogen uptake and retention will inform and improve water quality management within Spring Creek and other carp dominated streams. Additionally, documenting the patch-scale effects of carp engineering on macrophyte and macroinvertebrate diversity will help guide conservation efforts aimed at protecting and restoring biological communities within streams.

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APPENDIX

Taxa List of Macroinvertebrates Collected from the

Low Carp Biomass and High Carp Biomass Study Reaches of

Spring Creek, UT, 2008.

Phylum	Class	Order	Family	Genus	FFG
Arthropoda	Crustacea	Isopoda	Asellidae	Caecidotea	Collector-gatherer
Arthropoda	Arachnida	Acari (subclass)			Parasitic/ Predator
Arthropoda	Malacostraca	Amphipoda	Gammarida	Gammarus	Collector-gatherer
Arthropoda	Malacostraca	Amphipoda	Hyalellidae	Hyalella	Collector-gatherer
Arthropoda	Insecta	Coleoptera	Dytiscidae	Agabus	Predator
Arthropoda	Insecta	Coleoptera	Haliplidae	Brychius	Scraper
Arthropoda	Insecta	Coleoptera	Elmidae	Dubiraphia	Collector-gatherer
Arthropoda	Insecta	Diptera	Chironomidae	pupae	Collector-gatherer
Arthropoda	Insecta	Diptera	Empididae	Clinocera	Predator
Arthropoda	Malacostraca	Decapoda	Cambaridae	Orconectes	Collector-gatherer
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladiinae (subfamily)	Collector-gatherer
Arthropoda	Insecta	Diptera	Simuliidae		Collector-filterer
Arthropoda	Insecta	Diptera	Tabanidae		Predator
Arthropoda	Insecta	Diptera	Chironomidae	Tanypodinae (subfamily)	Predator
Arthropoda	Insecta	Diptera	Chironomidae	Tanytarsini (tribe within the subfamily chironominae)	Collector-gatherer
Arthropoda	Insecta	Ephemeroptera	Baetidae	Baetis	Collector-gatherer
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Ephemerella	Collector-gatherer
Annelida	Clitellata	Hirudinea (subclass)			Predator/CG

Phylum	Class	Order	Family	Genus	FFG
Arthropoda	Insecta	Hemiptera	Corixidae	Sigara/Corisella	Predator
Annelida	Clitellata	Oligochaeta (subclass)			Collector-gatherer
Mollusaca	Gastropoda	Basommatophora	Physidae		Collector-filterer
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Hydropsyche	Collector-filterer
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	Lepidostoma	Shredder
Arthropoda	Insecta	Trichoptera	Limnephilidae	Psychoglypha	Collector-gatherer
Platyhelminthes	Turbellaria				Predator
Mollusaca	Bivalvia	Veneroida	Pisidiidae	Pisidium	Collector-filterer
Arthropoda	Insecta	Zygoptera	Coenagrionidae	Amphiagrion	Predator